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Patterns of Bioluminescence in the Oceans

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April 23, 1981

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PATTERNS OF BIOLUMINESCENCE IN THE OCEANS

INTRODUCTION

Bioluminescence, or the emission of light by living organisms, is a world-wide phenomenon. It is caused by many creatures, the best-known of which is the firefly. However, there are a greater number and variety of luminous marine organisms than of luminous terrestrial or fresh-water organisms. Consequently, light in the sea is often seen.

Luminous marine species occur throughout the animal kingdom from the one-celled radiolarians to fish and squid. In the plant kingdom, only certain dinoflagellates are luminous. Some marine bacteria also luminesce. In some areas of the oceans, luminous species are the dominant forms of life. For example, below the photic zone of the ocean it has been estimated that 70% of the species and 90% of the individual organisms are luminous [1]. Even near the surface luminous species are frequent among the plankton. Furthermore many luminous midwater fish, most notably myctophids, and other organisms such as euphausiid crustaceans and squid migrate vertically to the surface at night to feed.

With such a diversity of luminous organisms, there are great variations in luminescence and at least five chemical mechanisms for producing light have been identified. Means of physiological control are as varied as the organisms themselves. The biological roles of luminescence are largely unknown, but several have been determined for a limited number of organisms. The intensity, kinetics and duration of the flash, patterns of flashing, and peak emission wavelength differ for each species. In fact, these characteristics are so species-dependent that it might be possible to identify the emitting organisms by measuring these five parameters.

Few luminous marine organisms have been studied in detail; consequently, little is known about the bioluminescent behavior and characteristics of the vast majority. The best source of information is the book *Bioluminescence* by E.N. Harvey [2]. This work has been updated for marine species in general by Tett and Kelly [3], Herring [4], and Kelly and Tett [5]. In addition, a bibliography with abstracts of individual papers on aspects of bioluminescence of naval interest, concentrating on work done since 1952, has been compiled [6] and a technical assessment of the bibliography prepared [7].

Most observations of bioluminescence at sea have simply been recorded as the presence of light and have not been concerned with the identification of the causative organisms. Displays have appeared to be both spontaneous, with no identifiable source of stimulation, and as the result of stimulation by mechanical means. Most luminous species can be expected to have only a limited geographical range but some higher groups (notably euphausiids, copepods, and dinoflagellates) appear to be universally distributed in the oceans [1].

Several previous studies based primarily on visual sightings have been made on the distribution and occurrence of marine bioluminescence. The earliest general studies were those of Smith [8,9], who examined the Meteorological Logs and Records of the Voluntary Observing Fleet from 1920-1930. Regional studies were made of the Okhotsk Sea [10], the Arabian Sea [11,12], the Atlantic Ocean [13], and the North Sea [14]. More recent general studies have been those of Turner [15,16], and Staples [17]. Turner [15] made the first attempt at statistically interpreting the sighting reports to identify areas of high bioluminescence by considering the shipping density as well as the number of sightings. Lynch [1] included in his report not only sightings but also instrumental observations and captures of known

luminous organisms. These reports concentrate on the spatial distribution of bioluminescence, and attempt to look at seasonal occurrences as well. Lynch [18] reviewed this literature and also discussed vertical distribution and diel variation of bioluminescence.

To be seen by the human eye, displays must be relatively bright. However, two instruments capable of detecting light intensities well below the threshold of the human eye have been used in marine bioluminescence research. Bathyphotometers are designed to measure light beneath the surface of the ocean. They may examine large or small volumes of water, may or may not provide their own source of stimulation, and may or may not be towable. Efforts are underway to design a floating bathyphotometer, capable of operating remotely in the manner of current meters. The second instrument is the low light level image intensifier (LLLII). These instruments can be used on surface ships or airplanes, and satellite-borne instruments are even being contemplated. They remotely sense dim bioluminescence, enhance it, and provide a picture of the display on a television screen. A ship apparently dark to the eye may be readily identifiable with a LLLII. These two sensors are more fully discussed by Lynch [1] and Hickman, *et al.* [7].

METHODS

For this report the studies on spatial and temporal distribution of bioluminescence cited above were reviewed. Reliance was placed on the statistical work of Turner [15,16] though he cited certain deficiencies in his own reports. Since these works are compilations of individual reports ranging in number from hundreds to thousands, it was not felt necessary to refer to the original individual reports. Tarasov [19] was consulted for Russian work before 1956 in the Black Sea. However, his analysis of world-wide distribution was ignored because of lack of accuracy in analyzing the data of Smith [8,9] and Glahn [13] and because of lack of documentation of original Russian data cited (see comments in [15]). For information on the luminous displays in the Arabian Sea, Kalle [20,21], Tett and Kelly [3], and Kelly and Tett [5] were consulted in addition to the works cited above. An analysis of the number and location of scientific studies of oceanic bioluminescence in Hickman, *et al.* [7] was also useful.

In estimating the frequency of bioluminescence encounters the author compared the number of reports from a given area with a rough estimate of the shipping density in that area. Because of lack of knowledge of exact shipping densities, a numerical analysis was not attempted. Because of the consensus that the Arabian Sea was the most luminescent region of the oceans, the author chose that as his standard for "very high frequency." Where shipping density was high, as in the Arabian Sea, but the number of reports was lower by approximately half, the author took this to be "high frequency." Another halving in the number of reports in dense shipping areas was taken to be "moderate frequency." Areas of dense shipping but few reports were considered to be "low frequency" areas. Overall, and especially in areas of little shipping, the author relied on his personal experience at sea, where he found bioluminescence in every location except one where measurements were attempted. Thus, the maps presented are somewhat subjective. It is unfortunate that existing data are too scanty to allow for a more reliable statistical presentation. However, the maps presented are of value in estimating the chances for encountering bioluminescence in a given area at a given time, provided that their limitations are understood.

RESULTS

Results are presented as a series of maps covering the Atlantic, Pacific, and Indian Oceans, with more detailed maps for the Mediterranean Sea and Gulf of Mexico-Caribbean Sea. Four maps, one for each season, are provided for each region. A fifth map is given to show the general density of reports for the region.

DISCUSSION AND CONCLUSIONS

Atlantic Ocean

Smith [8,9] analyzed the seasonal occurrence of bioluminescence in 10°-Marsden squares 145-151, which span the Atlantic from Nova Scotia to the coast of France. He found low levels of bioluminescence in winter throughout, and a tendency to peak in spring off Newfoundland and in summer near the European coast. In the mid-Atlantic no seasonal peak could be distinguished. Glahn [13] studied 10°-squares between the latitudes 0° and 60° and found a tendency for bioluminescence to peak in the spring and early summer in the high latitudes of the North Atlantic. Nearer the equator and throughout the South Atlantic occurrence appeared fairly even throughout the year. Staples [17] agreed with Glahn. In addition, he observed that luminescence in the coastal waters of the British Isles and the Scandinavian Peninsula was associated with dinoflagellate blooms, which tend to occur in late spring and early fall. Lynch [1], while agreeing with the works cited above, noted that luminescence was often associated with red tides off the coasts of New England and Florida. Red tides, which are nothing more than unusually heavy dinoflagellate blooms, may occur throughout the year but are most frequent in late spring and early fall. Near the equator all the above authors and Turner [15,16] agreed that bioluminescence occurred fairly evenly throughout the year and at relatively high levels. Data for the South Atlantic are relatively sparse, but Smith, Glahn, Staples, and Turner all agreed that the area near the mouth of the Rio de la Plata was very bright throughout the year. Lynch has noted moderate luminescence off Namibia during three quarters of the year. In the Atlantic, no correlation has been definitely established between the occurrence of bioluminescence and any physical or meteorological phenomena other than dinoflagellate blooms. These analyses are reflected in Figs. 1 through 5.

Shipping in the North Atlantic between Europe and North America, near the equator between South America and Africa, and along the continental coasts is very dense. Thus, considerable reliance can be placed on the accuracy of the maps in these regions. In the far North Atlantic and most of the South Atlantic, shipping is much less dense. Therefore the maps are considerably less reliable in these areas.

Gulf of Mexico and Caribbean Sea

Bioluminescence frequency in the Gulf of Mexico is largely unknown, except along the coasts of the United States where it is frequently associated with red tides. Staples [17] and Lynch [1] have indicated that bioluminescence occurred throughout the year, but less in winter than at other times. Smith [8,9] and Turner [15,16] counted relatively few reports for the region. Shipping was infrequent in the western Gulf, but high in the eastern Gulf and along the coast.

In the Caribbean Sea, shipping was dense throughout. Smith, Staples and Turner counted moderate numbers of reports in this region, although Lynch indicated high numbers. Staples and Lynch indicated that bioluminescence occurred fairly evenly throughout the year. Three areas in the Caribbean showed constant high levels of bioluminescence. These were the shallow luminous bays of Puerto Rico and Jamaica. In these bays permanent colonies of luminous dinoflagellates exist in bloom conditions. Data for these regions are shown in Figs. 6 through 10.

Mediterranean and Black Seas

In the Mediterranean Sea bioluminescence seemed to occur with moderate frequency throughout the year, according to Smith [8,9], Turner [15,16], and Lynch [1]. Glahn [13] suggested that a bioluminescence maximum occurred in spring, while Staples [17] indicated that a minimum occurred in summer. All the above authors agreed, however, that the western Mediterranean was brighter than the eastern, and that the area near the Strait of Gibraltar was especially bright.

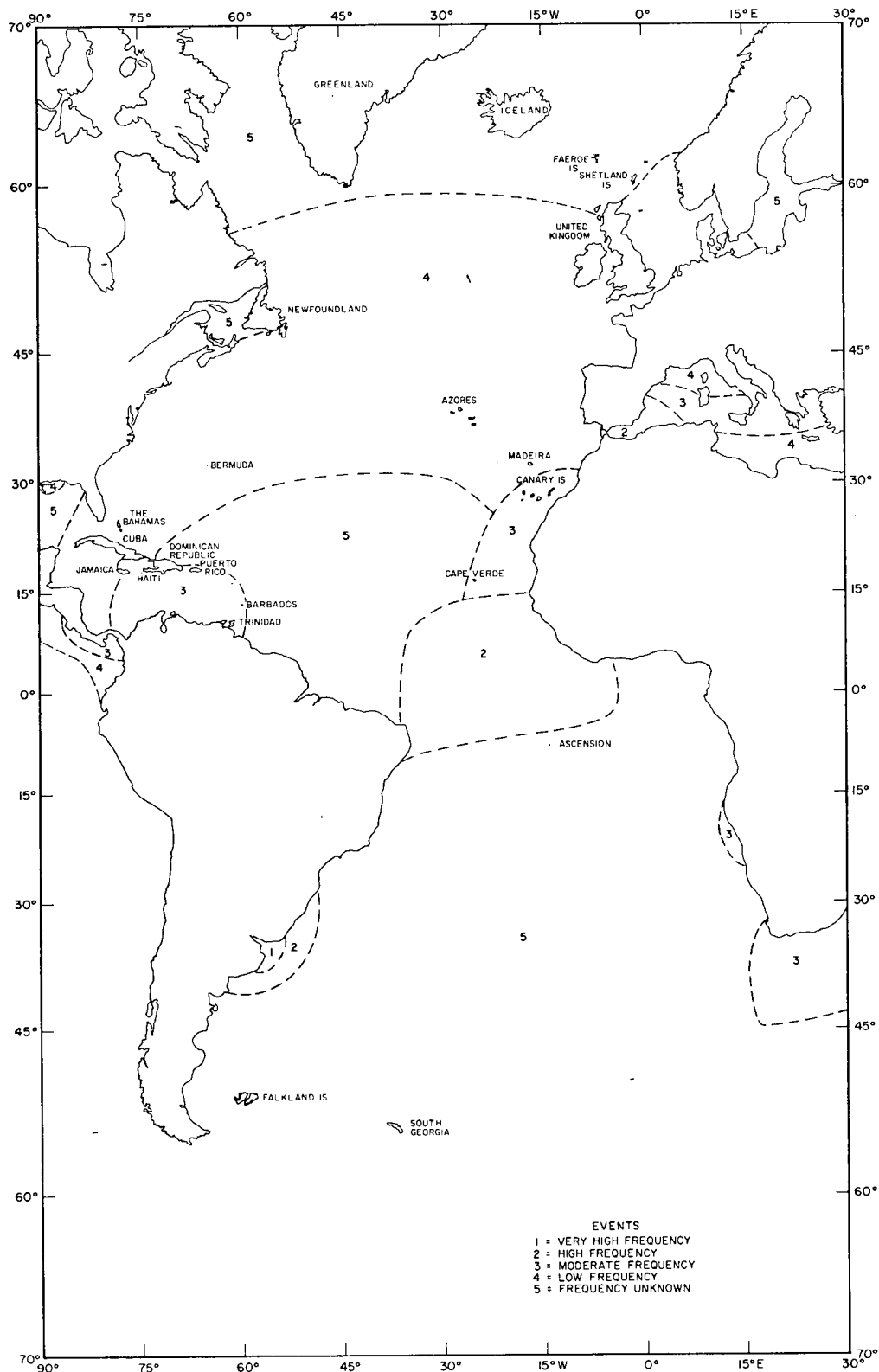


Fig. 1 — Frequency of bioluminescence encounters in the Atlantic Ocean, Jan. through Mar.

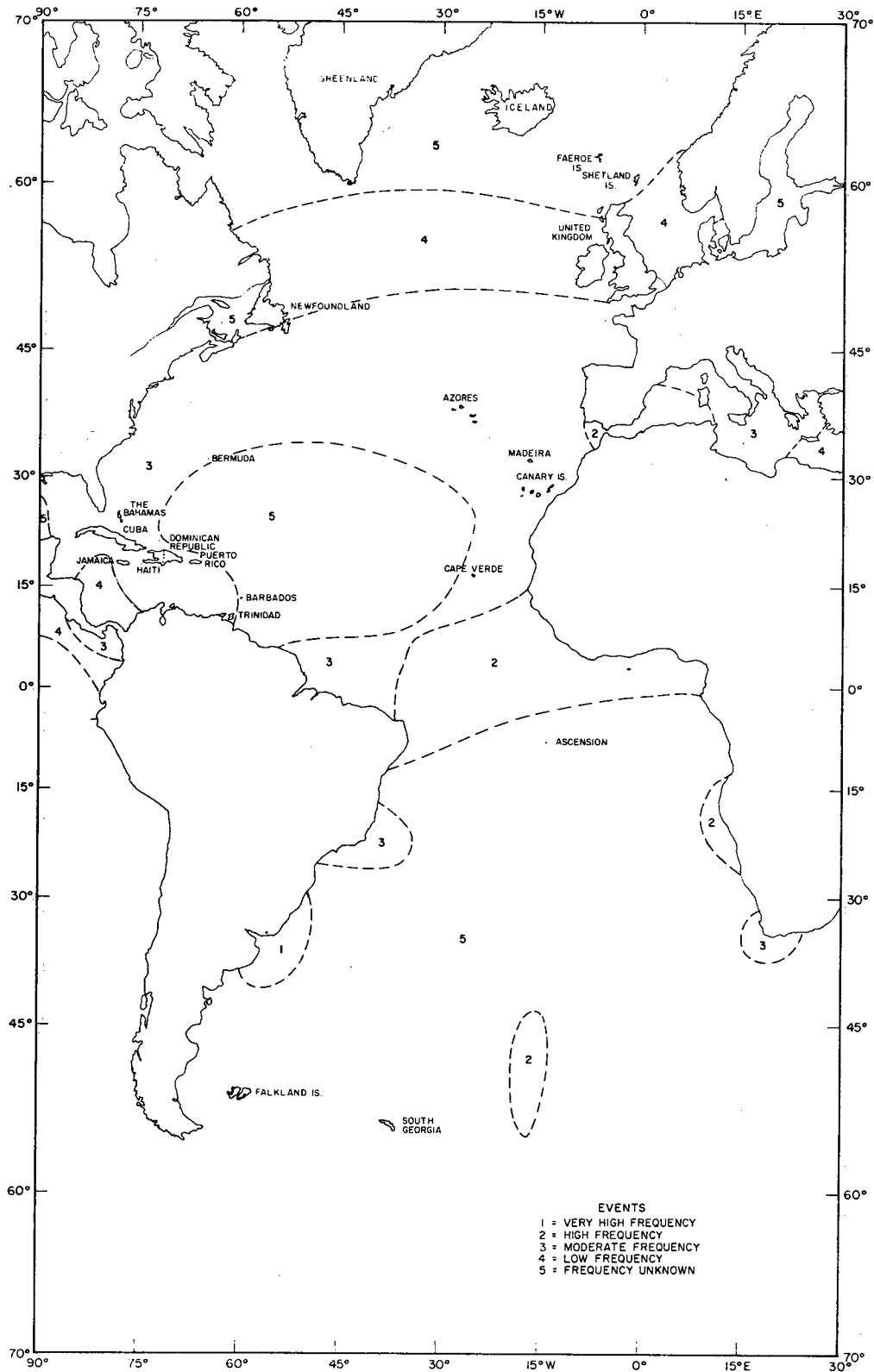


Fig. 2 — Frequency of bioluminescence encounters in the Atlantic Ocean, Apr. through June.

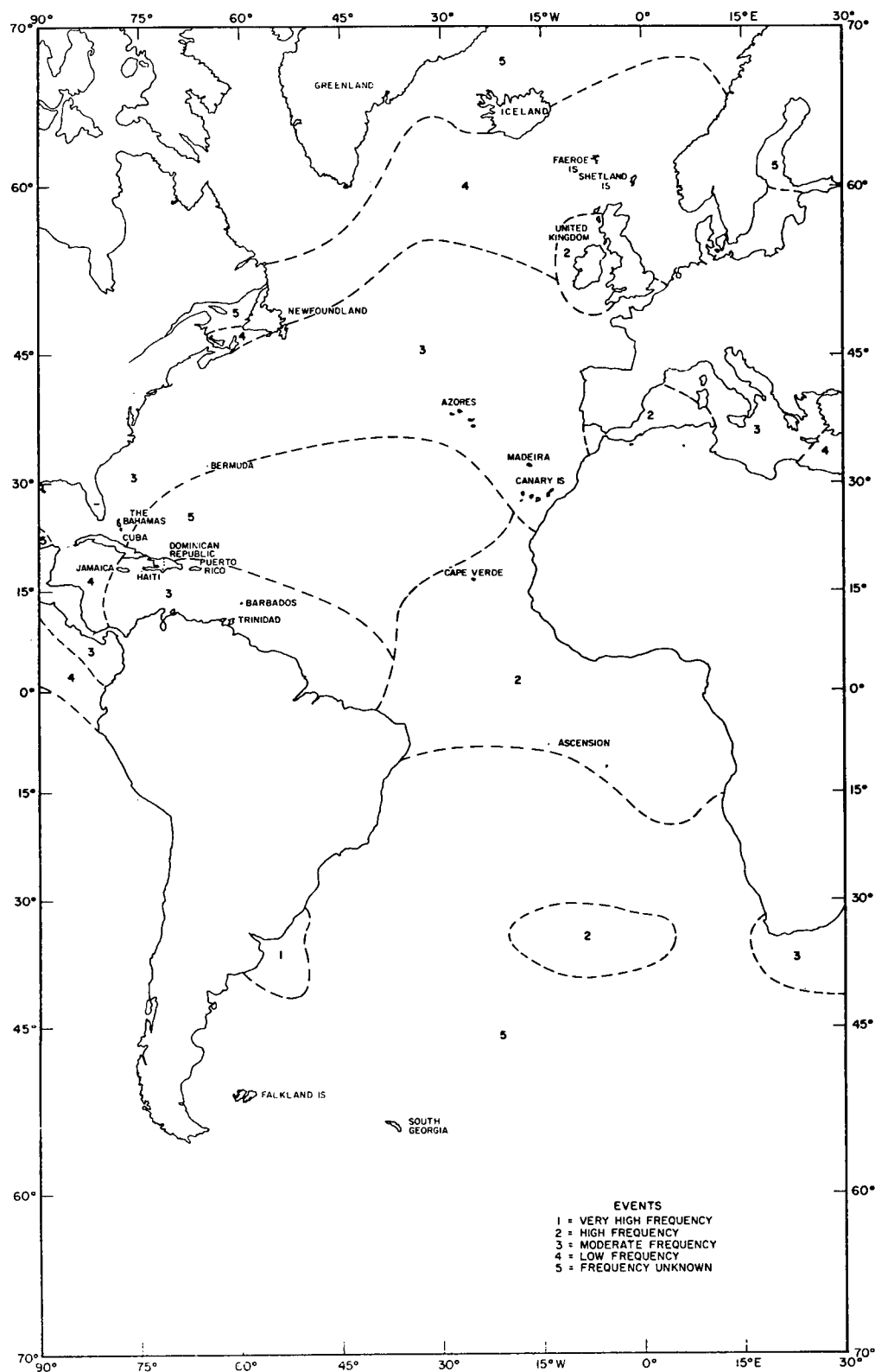


Fig. 3 — Frequency of bioluminescence encounters in the Atlantic Ocean, July through Sept.

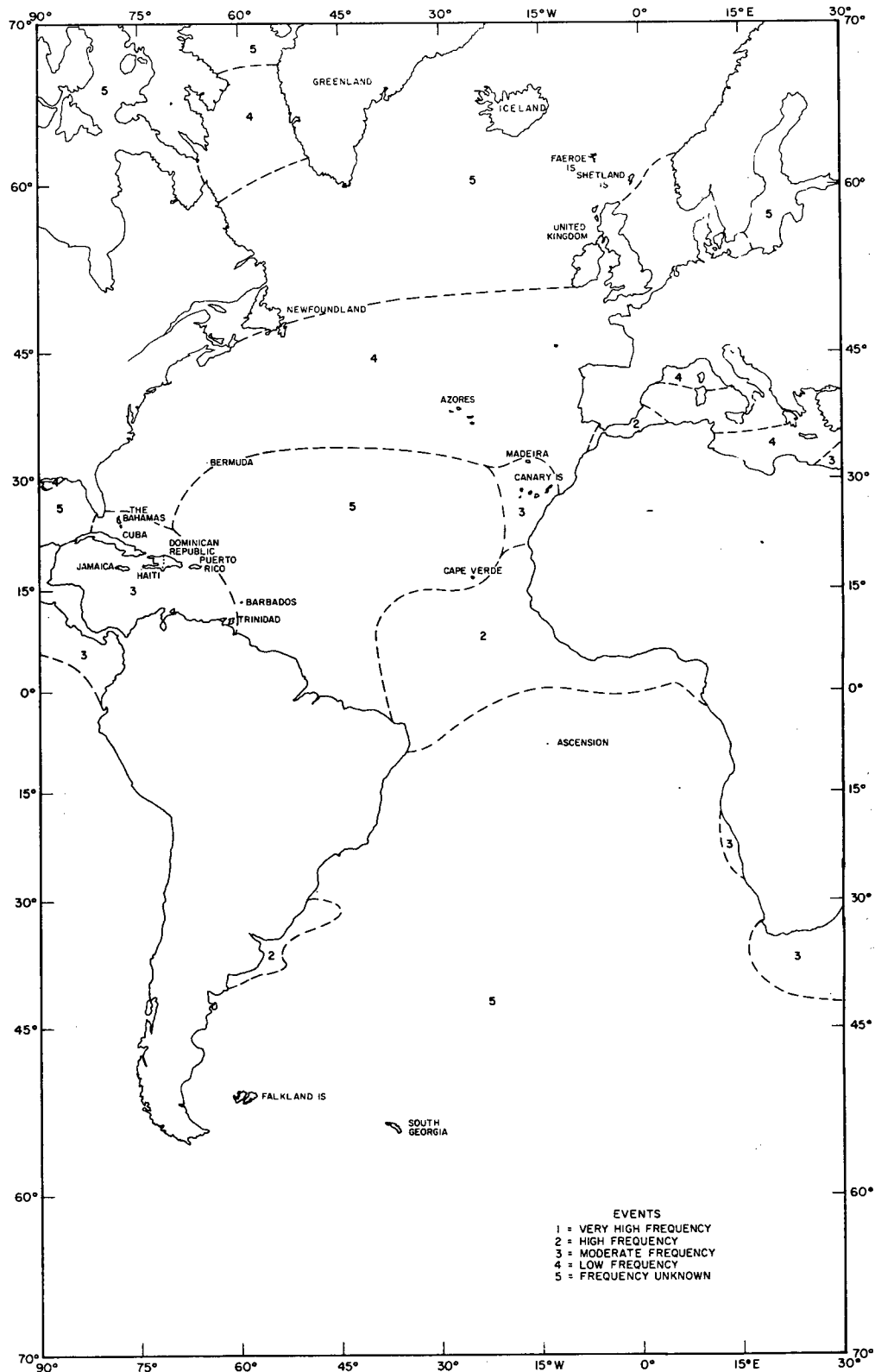


Fig. 4 — Frequency of bioluminescence encounters in the Atlantic Ocean, Oct. through Dec.

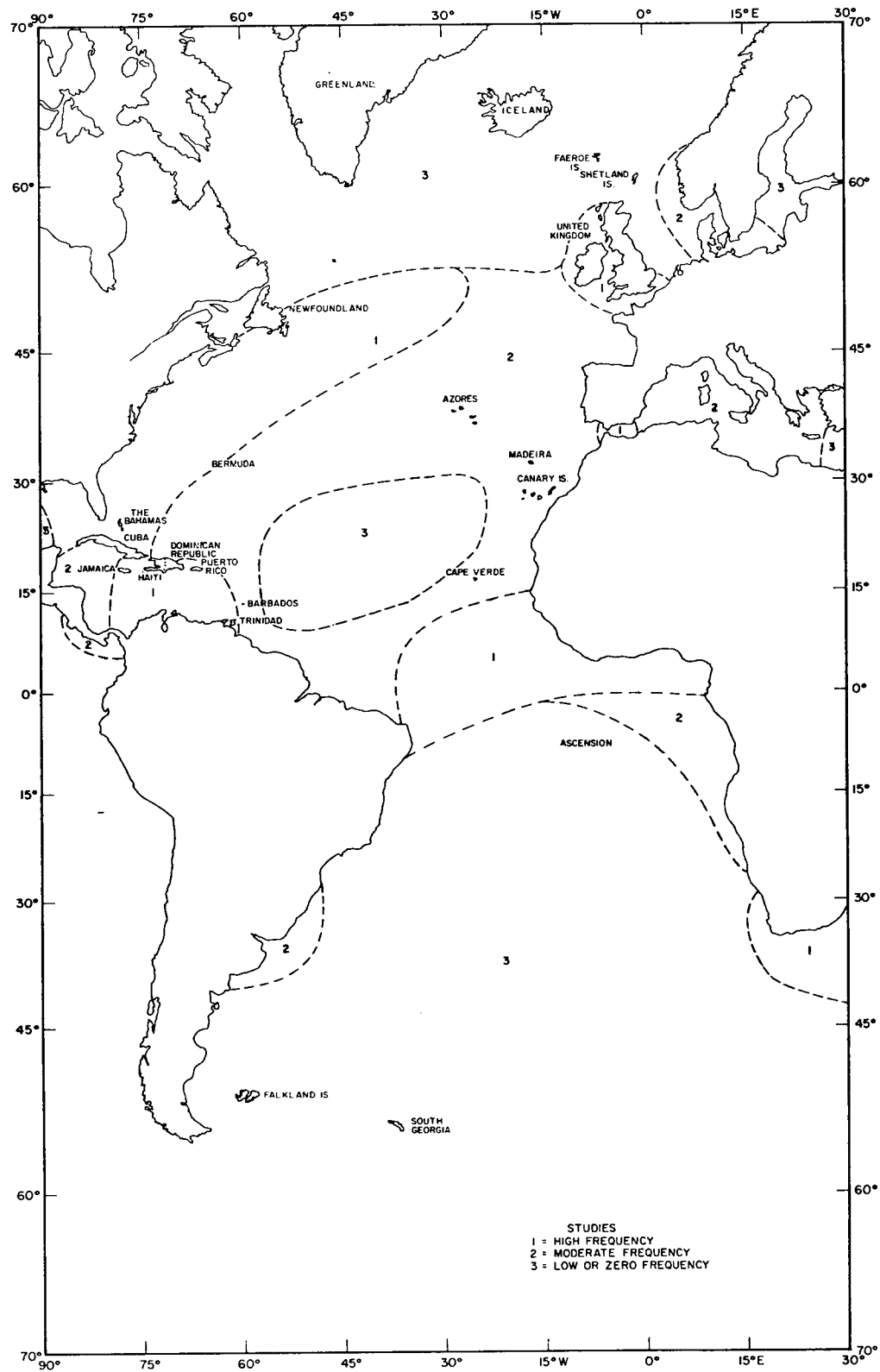


Fig. 5 — Frequency of bioluminescence reports in the Atlantic Ocean

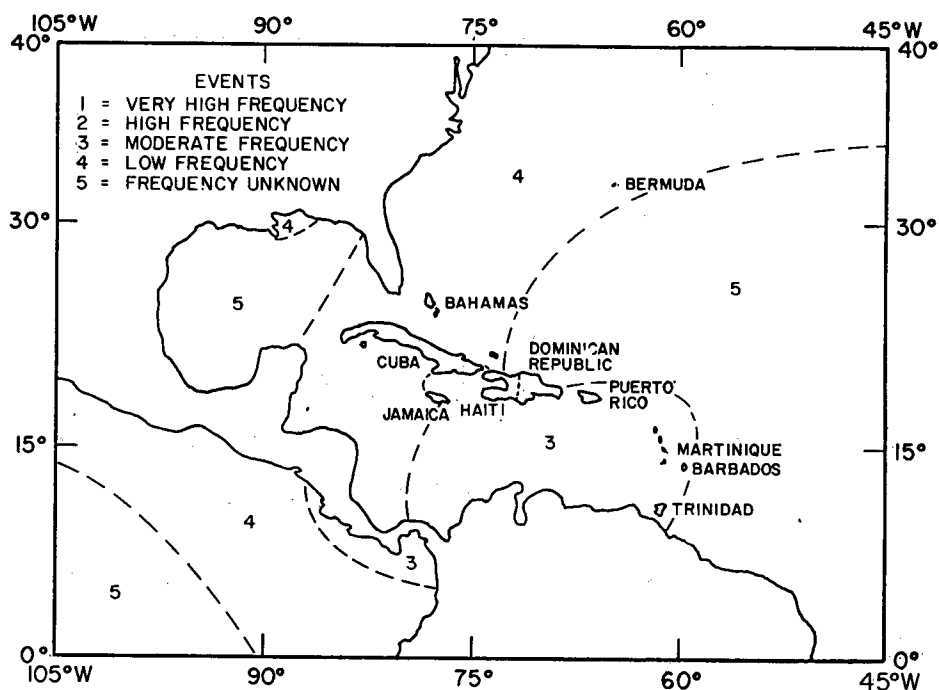


Fig. 6 — Frequency of bioluminescence encounters in the Gulf of Mexico and Caribbean Sea, Jan. through Mar.

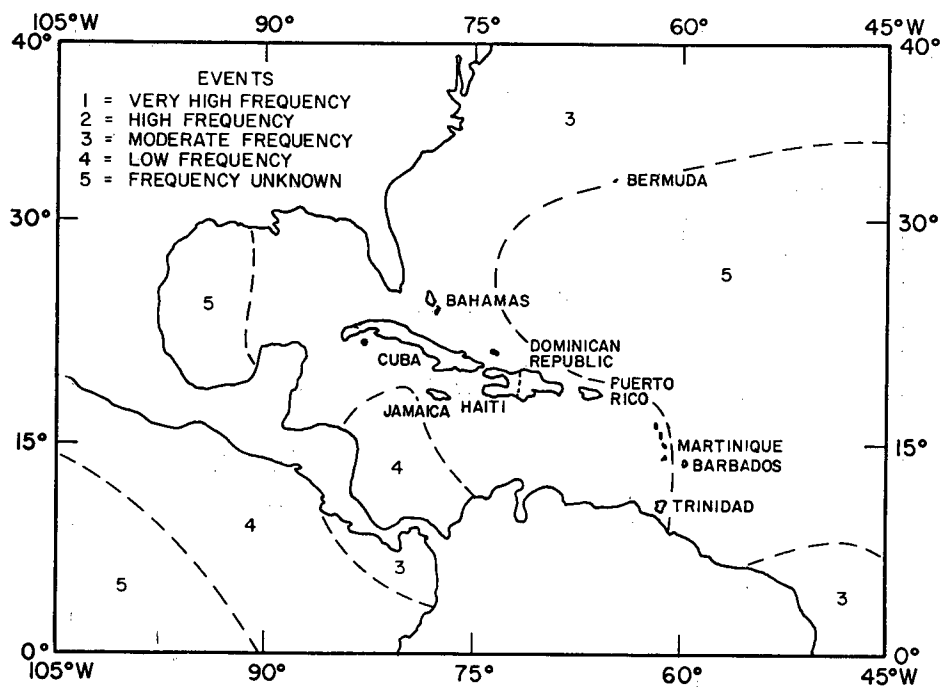


Fig. 7 — Frequency of bioluminescence encounters in the Gulf of Mexico and Caribbean Sea, Apr. through June

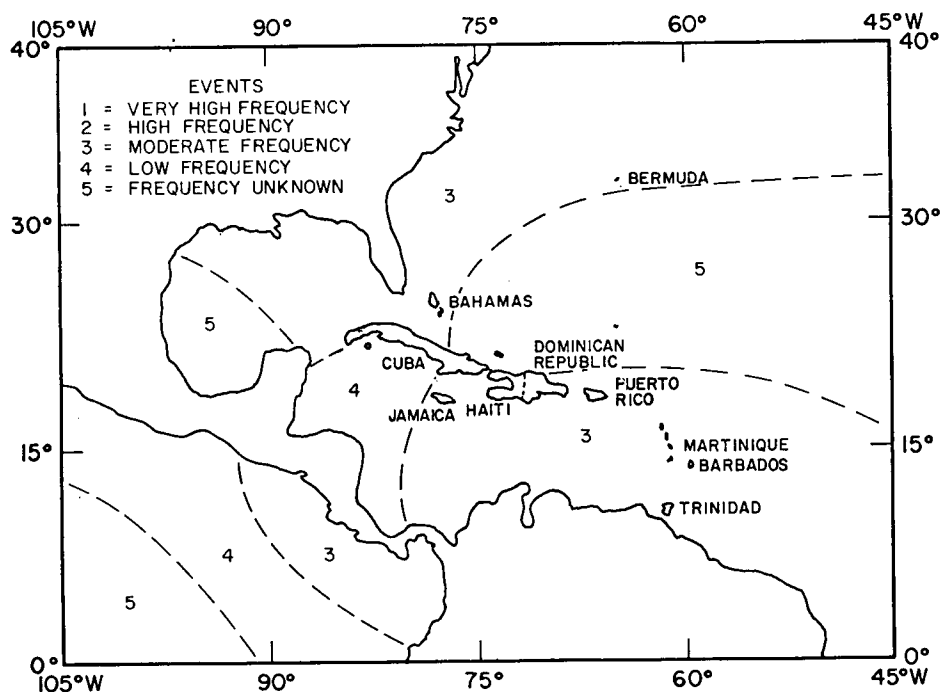


Fig. 8 — Frequency of bioluminescence encounters in the Gulf of Mexico and Caribbean Sea, July through Sept.

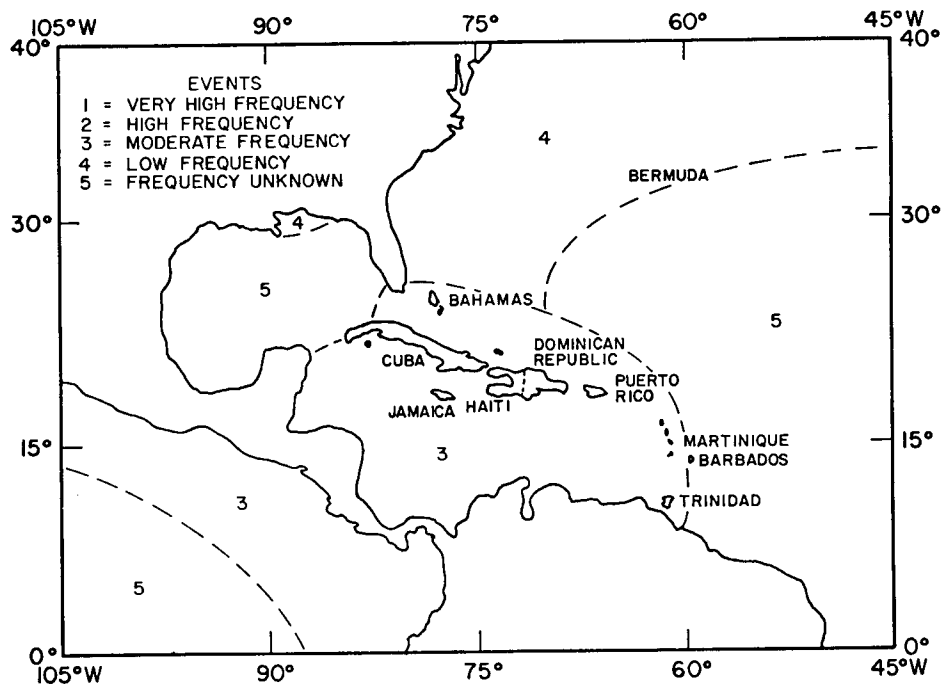


Fig. 9 — Frequency of bioluminescence encounters in the Gulf of Mexico and Caribbean Sea, Oct. through Dec.

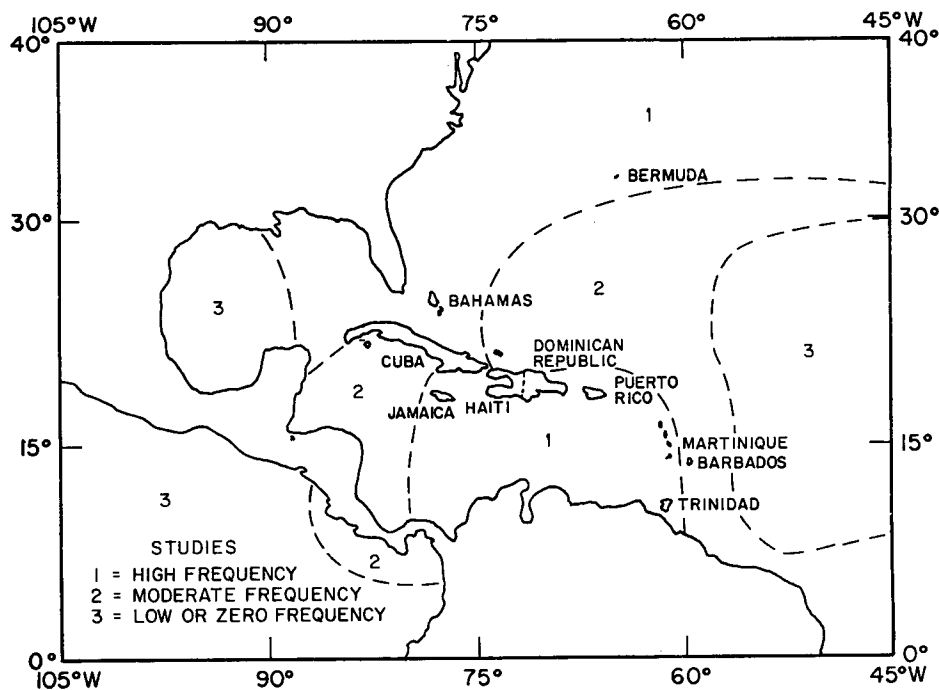


Fig. 10 — Frequency of bioluminescence reports in the Gulf of Mexico and Caribbean Sea

In the Black Sea, Tarasov [19] and Lynch [1] both indicated that bioluminescence occurred all year long around the Crimean peninsula, with frequencies of encounters greater during summer than winter. However, bioluminescence has been studied in the southern part of the Black Sea only in summer, and its frequency is unknown for the rest of the year. Data for these regions are shown in Figs. 11 through 15.

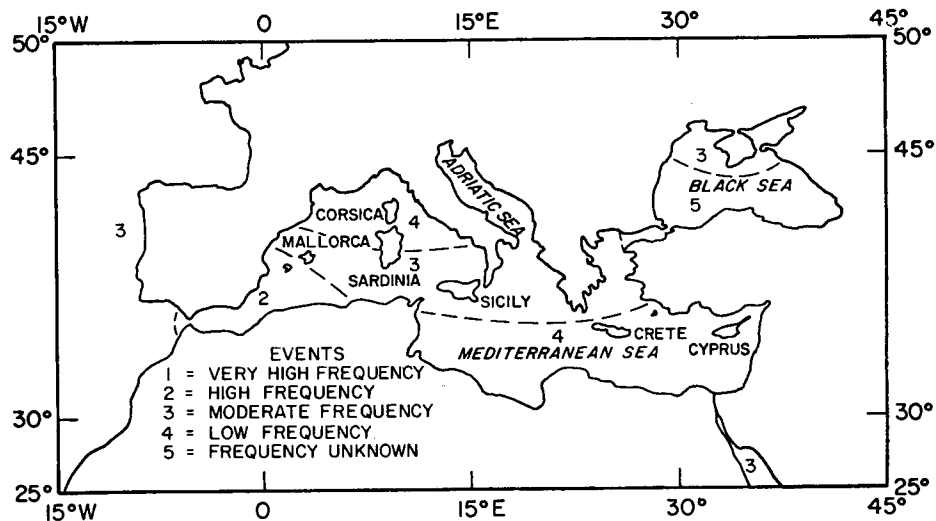


Fig. 11 — Frequency of bioluminescence encounters in the Mediterranean and Black Seas, Jan. through Mar.

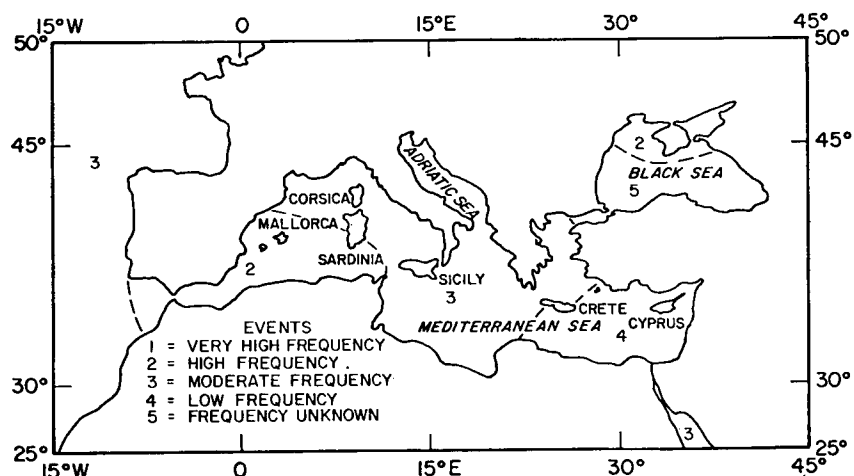


Fig. 12 — Frequency of bioluminescence encounters in the Mediterranean and Black Seas, Apr. through June

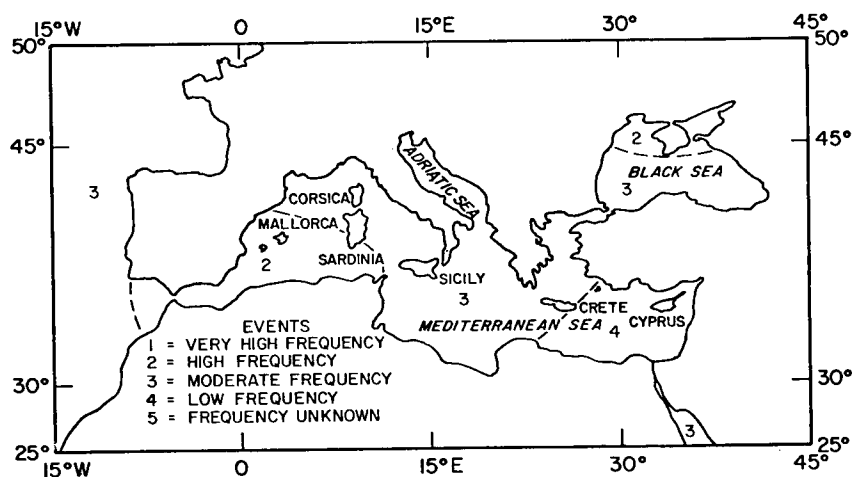


Fig. 13 — Frequency of bioluminescence encounters in the Mediterranean and Black Seas, July through Sept.

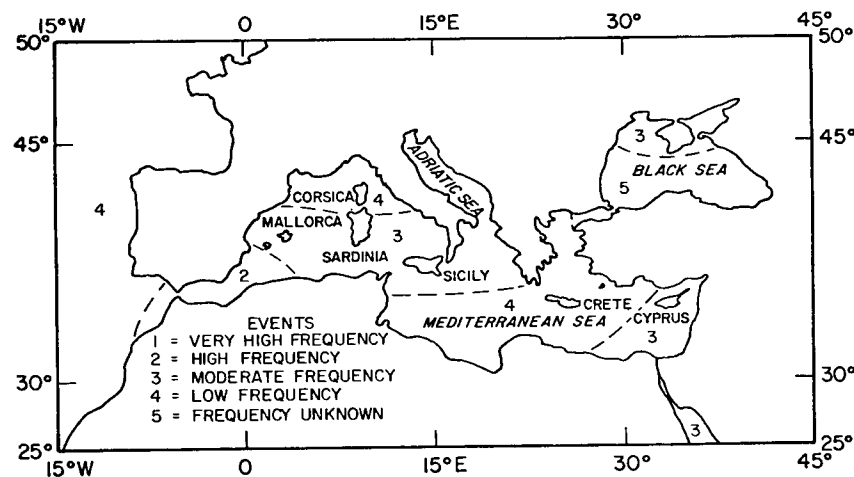


Fig. 14 — Frequency of bioluminescence encounters in the Mediterranean and Black Seas, Oct. through Dec.

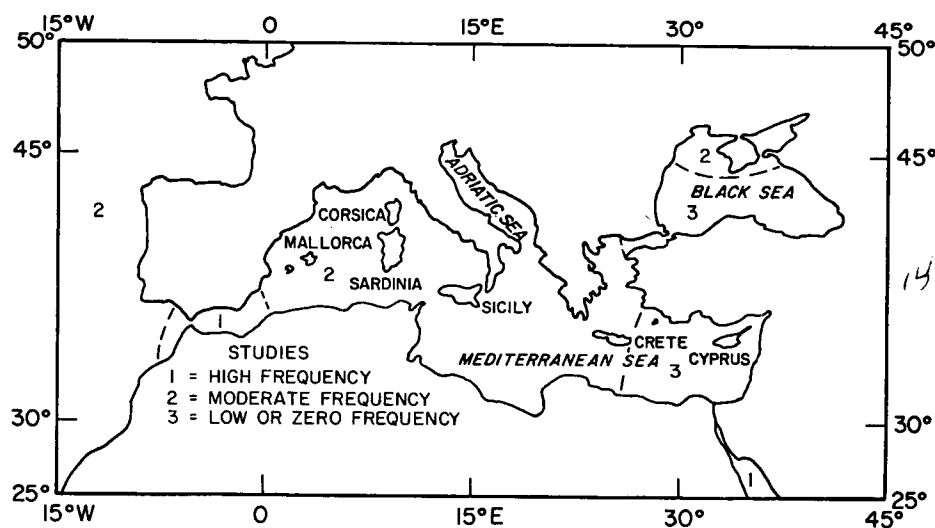


Fig. 15 — Frequency of bioluminescence reports in the Mediterranean and Black Seas

Pacific Ocean

Data for the eastern Pacific region are shown in Figs. 16 through 20; for the central Pacific in Figs. 21 through 25; and for the western Pacific in Figs. 26 through 30. Shipping in the Pacific is fairly dense along the continental coasts, around Hawaii and in Japan, the Philippines and Indonesia. However, there are vast areas, especially southeast of New Zealand and the Society Islands, where shipping is extremely sparse. Likewise, reports of bioluminescence in the Pacific are relatively few, most coming from near the Panama Canal, along the coast of the contiguous United States, near Hawaii, Japan and New Guinea, and in the South China Sea. This information is shown in Figs. 20, 25 and 30.

Glahn [13] performed a seasonal analysis on his Pacific data for comparison to his Atlantic data and found bioluminescence minimal in both the North and South Pacific in their respective winters. These minima were more pronounced at higher latitudes. Near the equator bioluminescence occurred fairly steadily throughout the year. These findings were supported by Staples [17] and Lynch [1], who also noted bioluminescence maxima along the California coast and around Japan in late spring and summer. In addition, Lynch noted the frequent association of luminescence with red tides in both locations. In the Sea of Okhotsk, Stukalin [10] observed bioluminescence all year around, even in broken ice fields in winter. However, there was a maximum in August through September.

Turner [15,16] and Staples [17] agreed that bioluminescence was fairly common in the South China Sea. In addition, Turner performed a seasonal analysis for four regions within the South China Sea and for the sea as a whole. He found relatively constant levels of bioluminescence throughout the year, with a slight apparent maximum in October through November. However, because of the small number of reports available he considered this maximum an artifact resulting from the inadequacy of the data.

Indian Ocean

The consensus of all who have studied the world-wide distribution of bioluminescence is that the Arabian Sea and nearby waters are the brightest regions in the oceans. The Bay of Bengal and the Strait of Malacca are also unusually rich in luminescence. Furthermore, this brightness extends throughout the year. But Smith [8,9], Glahn [13], and Anonymous [11] showed a bioluminescence maximum in late summer and early fall. This maximum appeared to be correlated with the time of greatest current

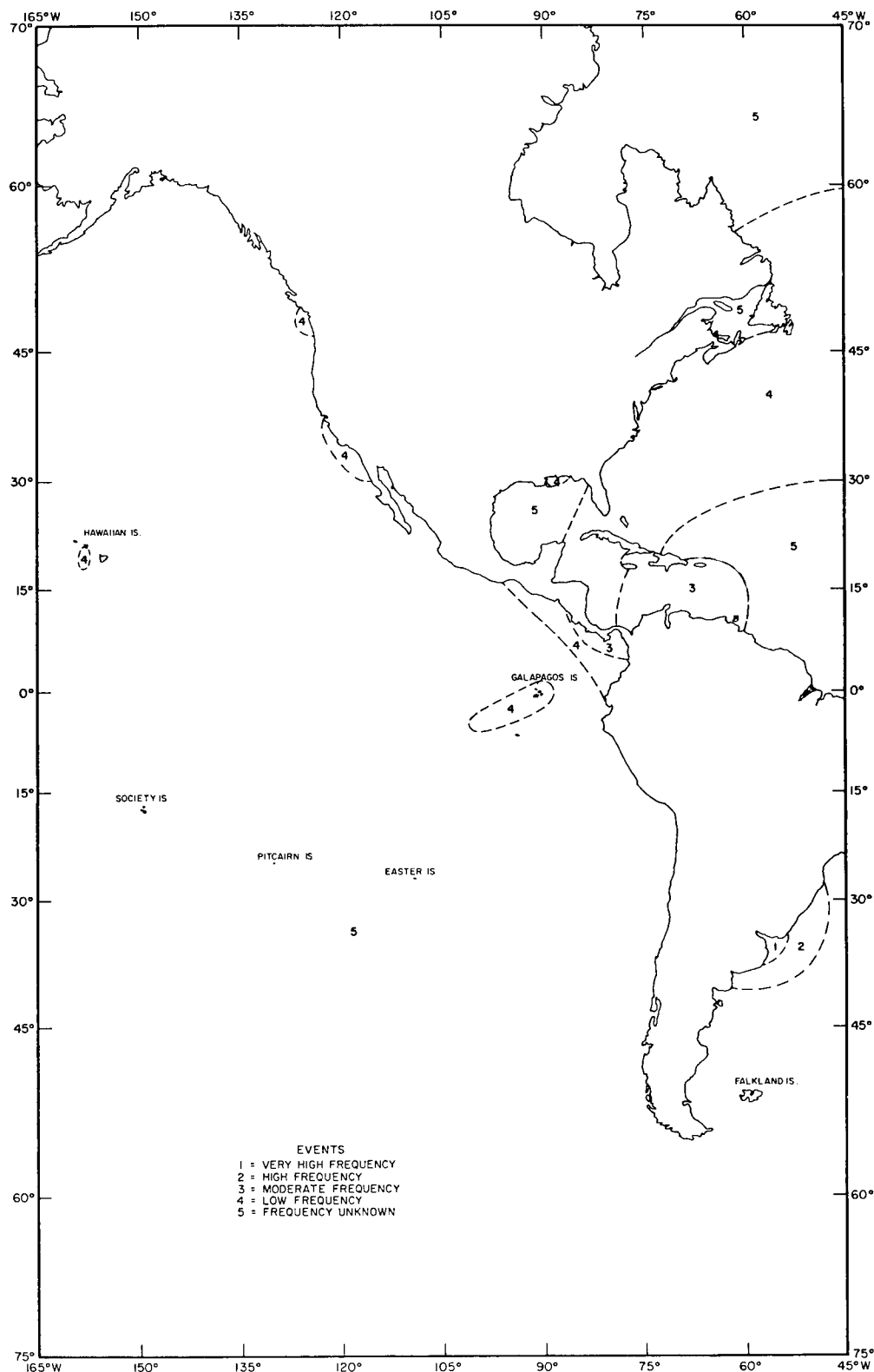


Fig. 16 — Frequency of bioluminescence encounters in the Eastern Pacific Ocean, Jan. through Mar.

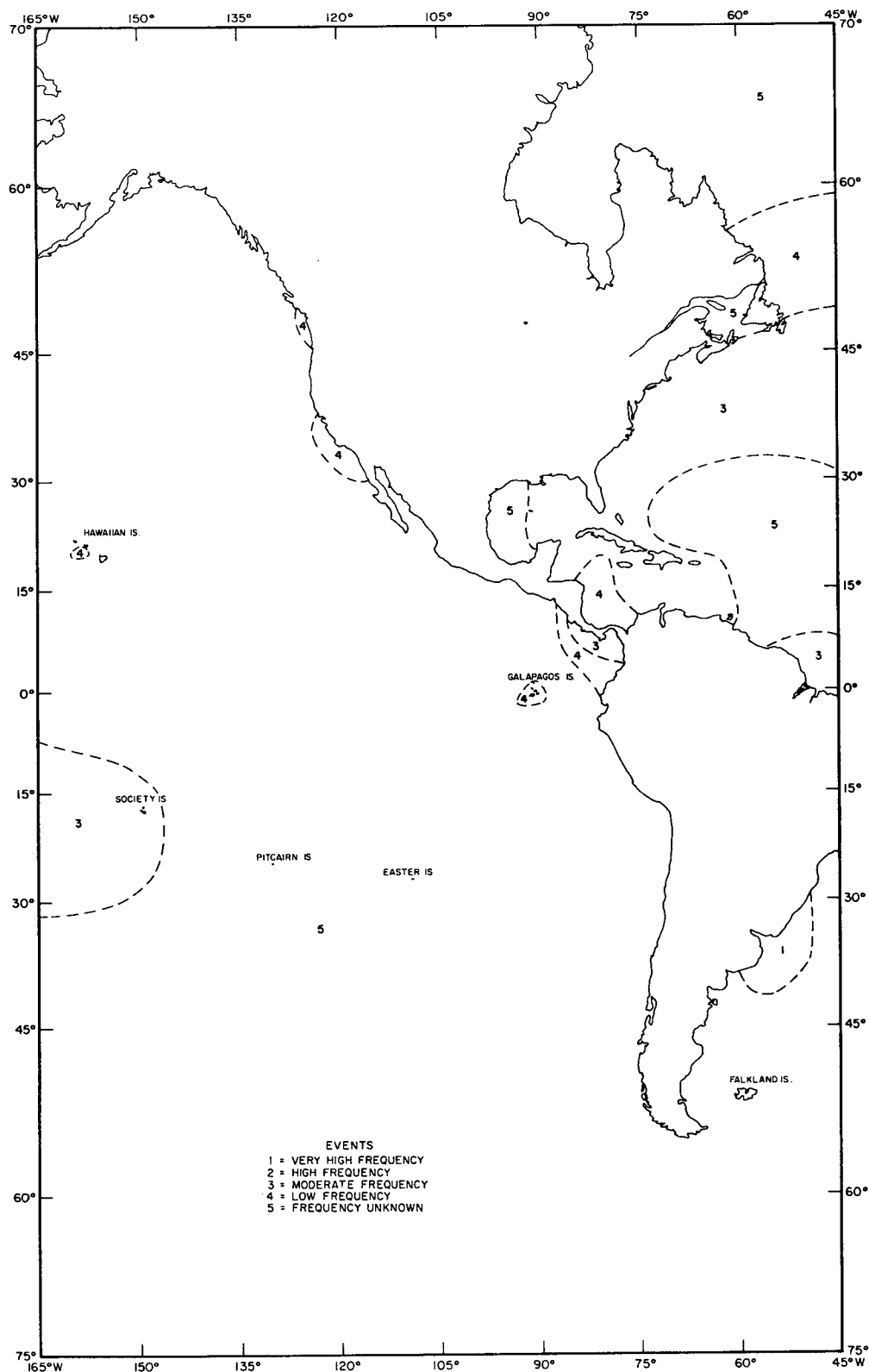


Fig. 17 — Frequency of bioluminescence encounters in the Eastern Pacific Ocean, Apr. through June

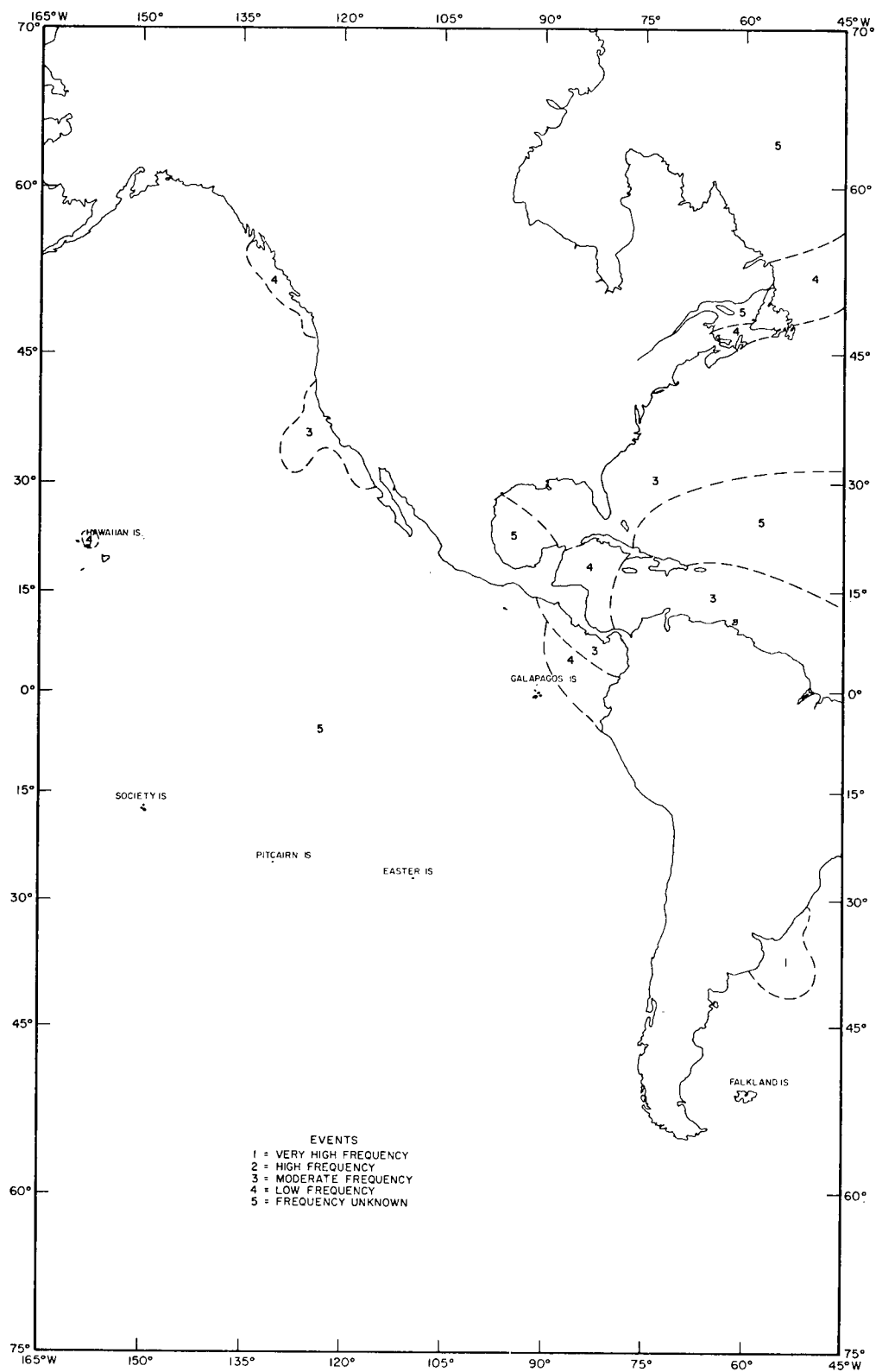


Fig. 18 — Frequency of bioluminescence encounters in the Eastern Pacific Ocean, July through Sept.

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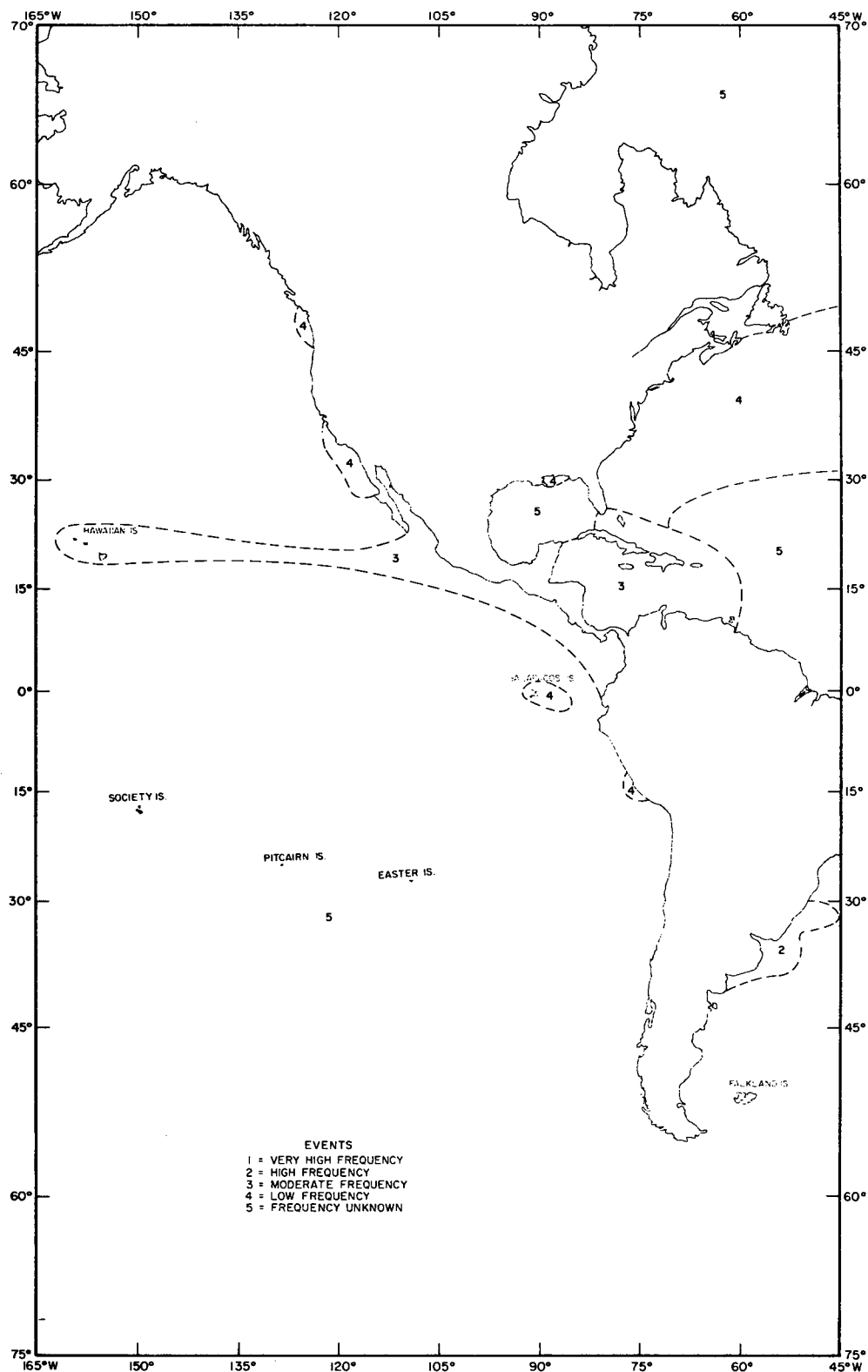


Fig. 19 — Frequency of bioluminescence encounters in the Eastern Pacific Ocean, Oct. through Dec.

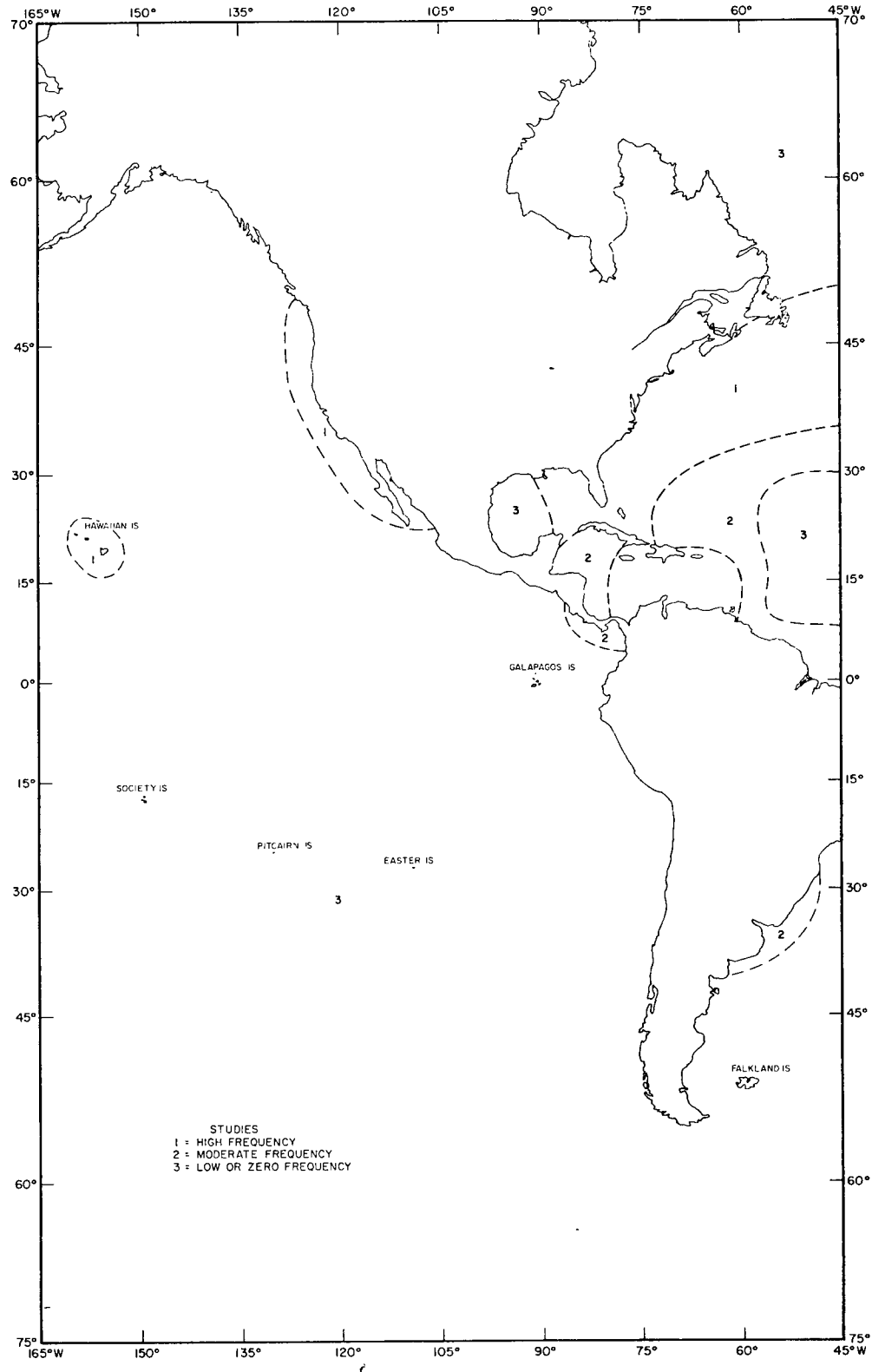


Fig. 20 — Frequency of bioluminescence reports in the Eastern Pacific Ocean

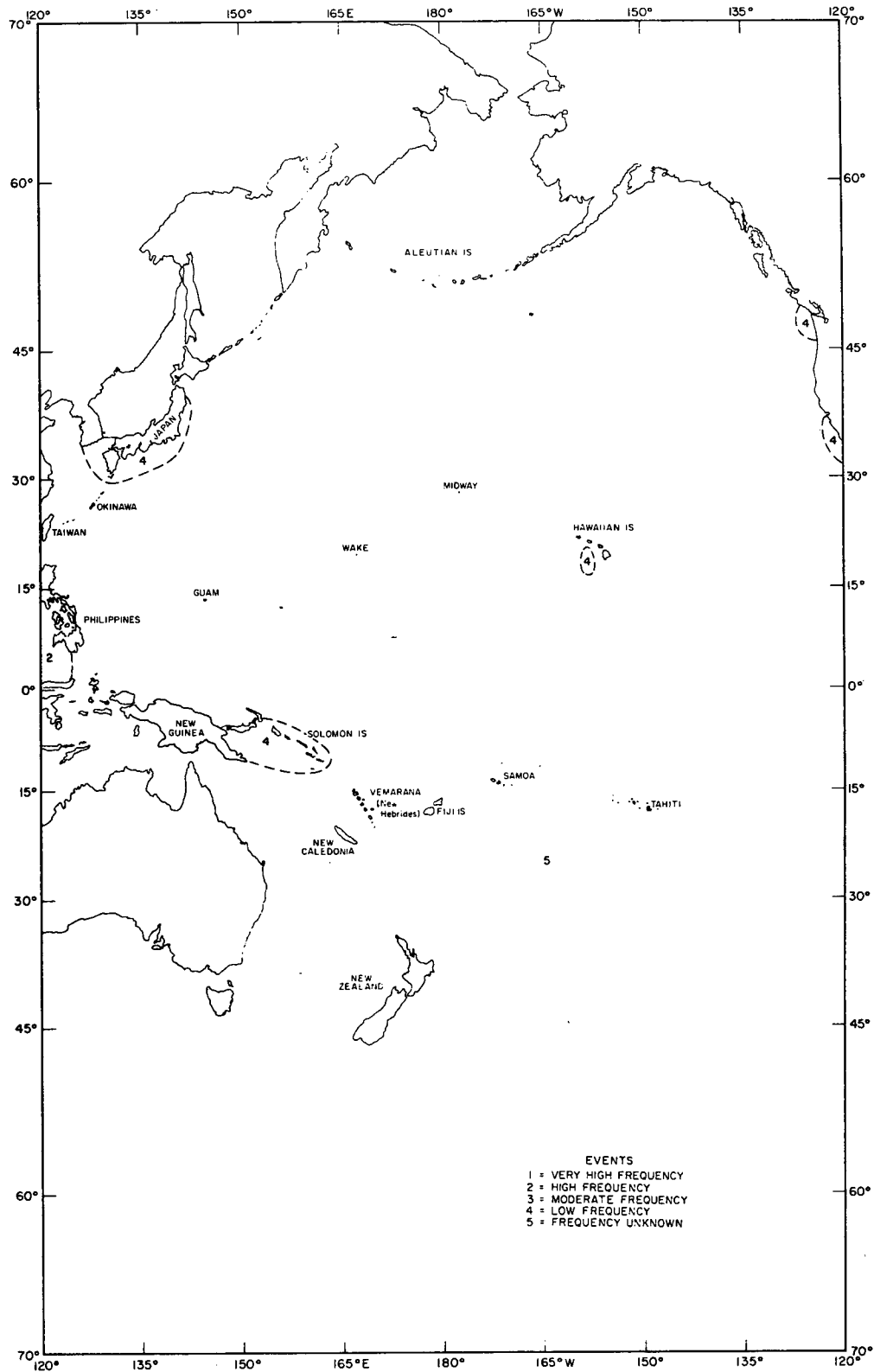


Fig. 21 — Frequency of bioluminescence encounters in the Central Pacific Ocean, Jan. through Mar.

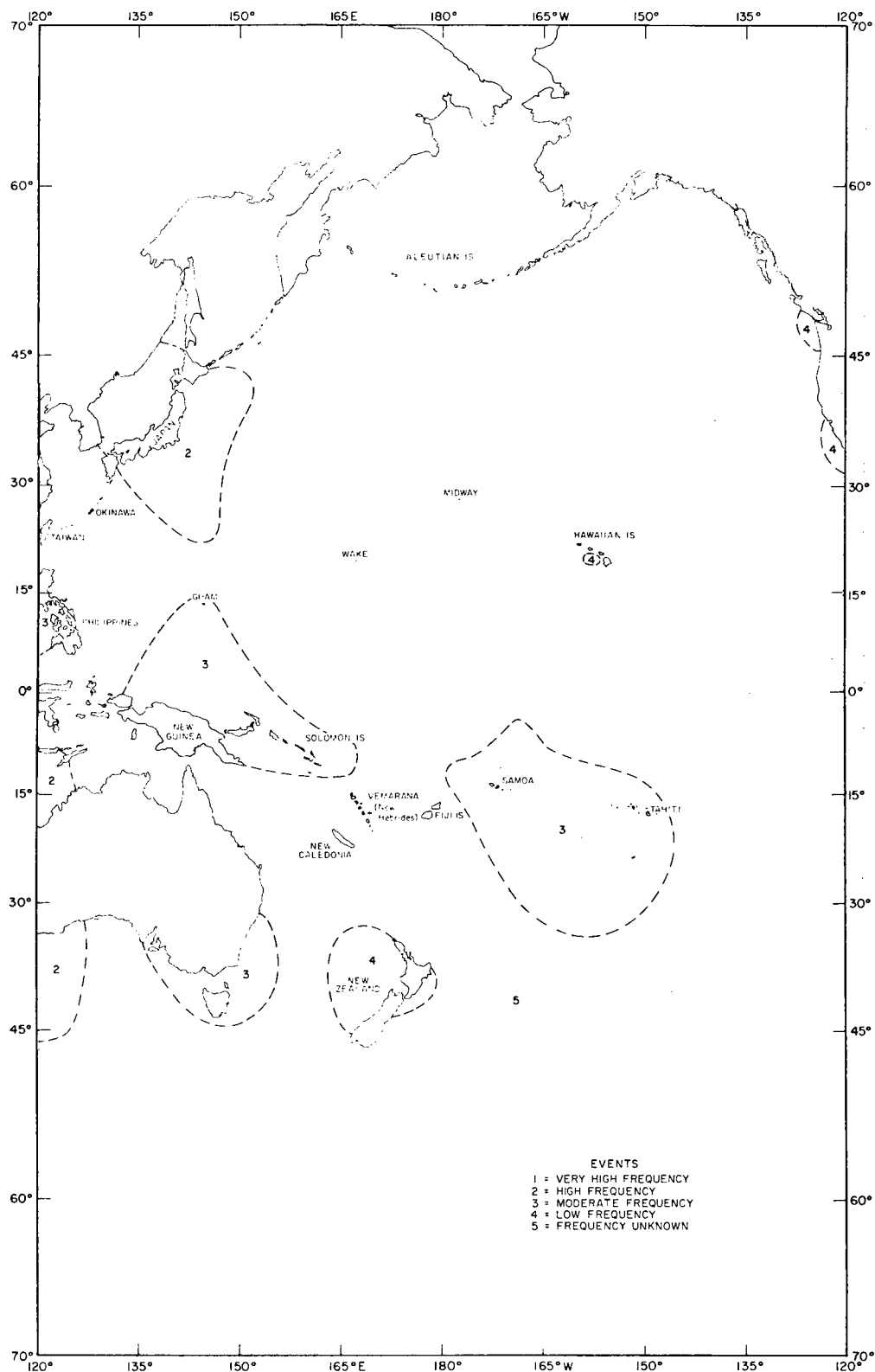


Fig. 22 — Frequency of bioluminescence encounters in the Central Pacific Ocean, Apr. through June

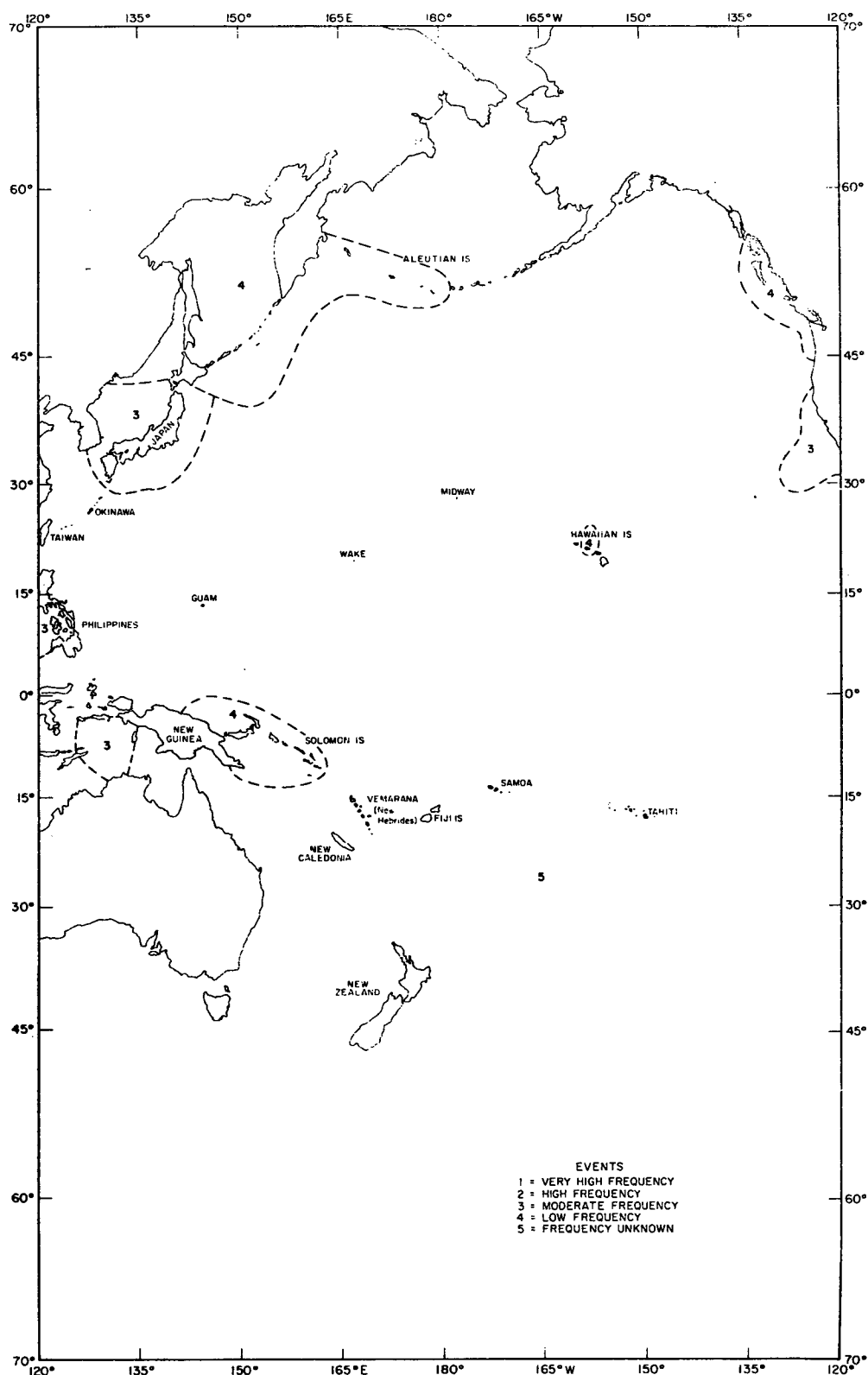


Fig. 23 — Frequency of bioluminescence encounters in the Central Pacific Ocean, July through Sept.

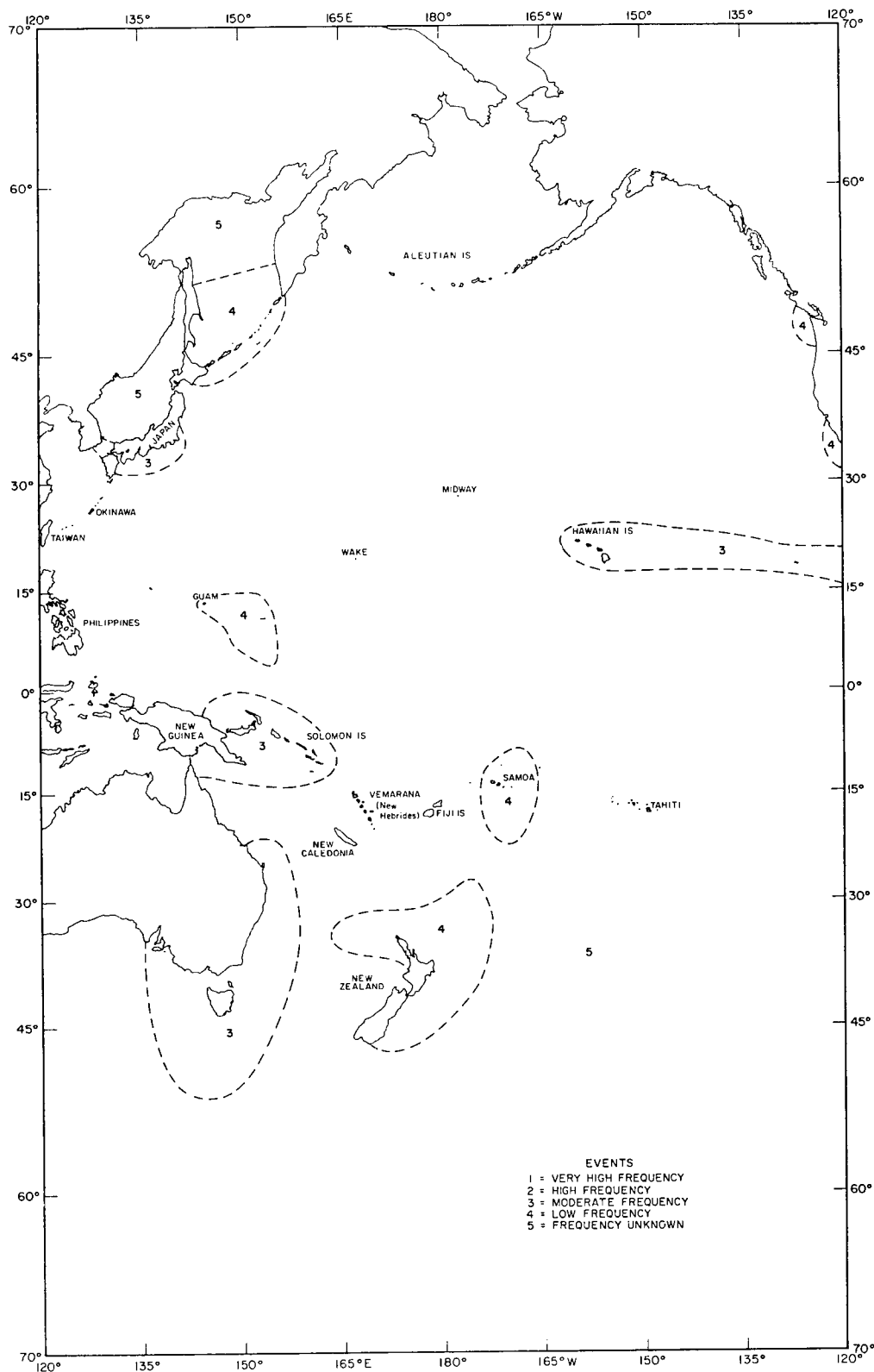


Fig. 24 — Frequency of bioluminescence encounters in the Central Pacific Ocean, Oct. through Dec.

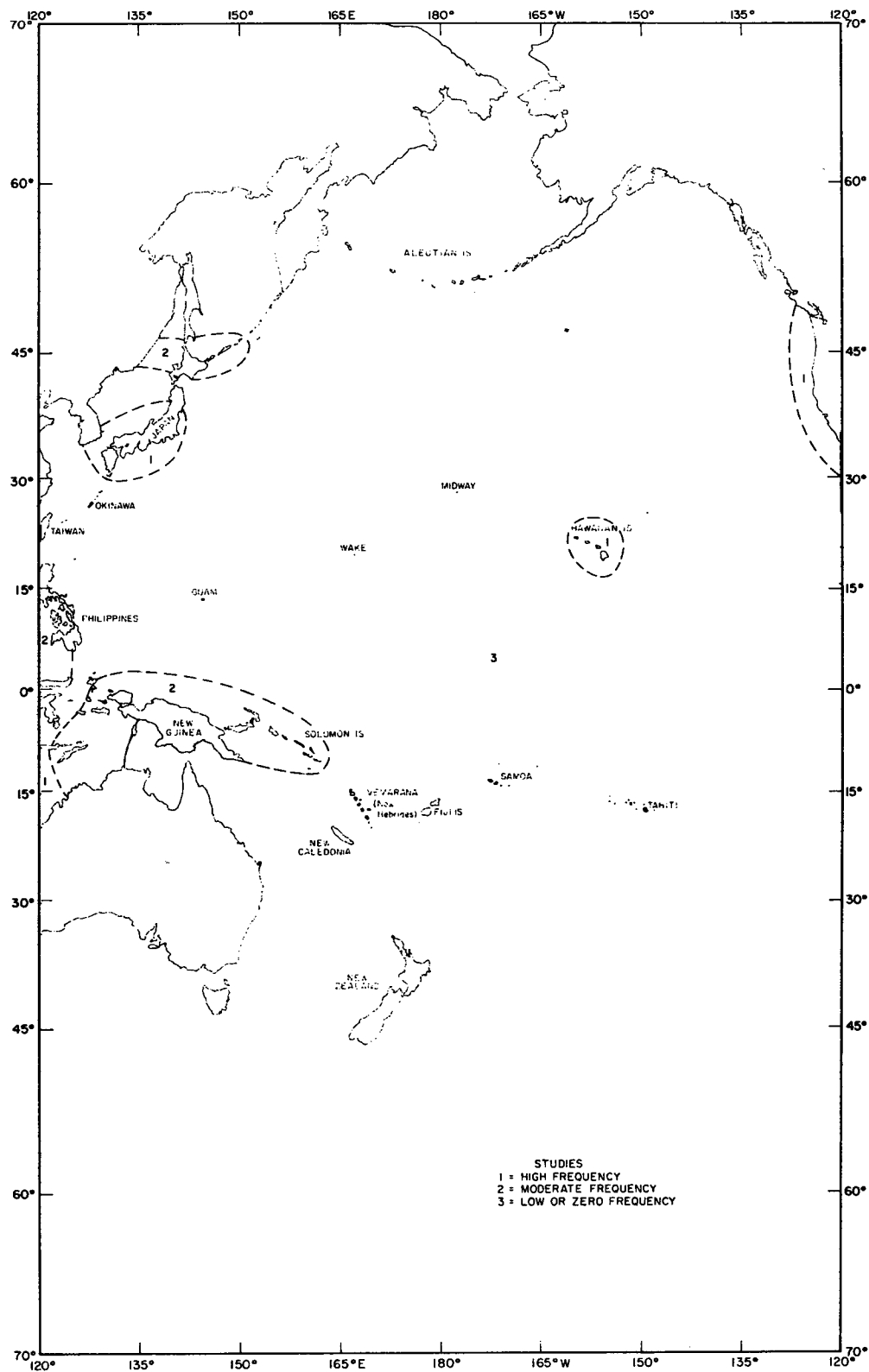


Fig. 25 — Frequency of bioluminescence reports in the Central Pacific Ocean

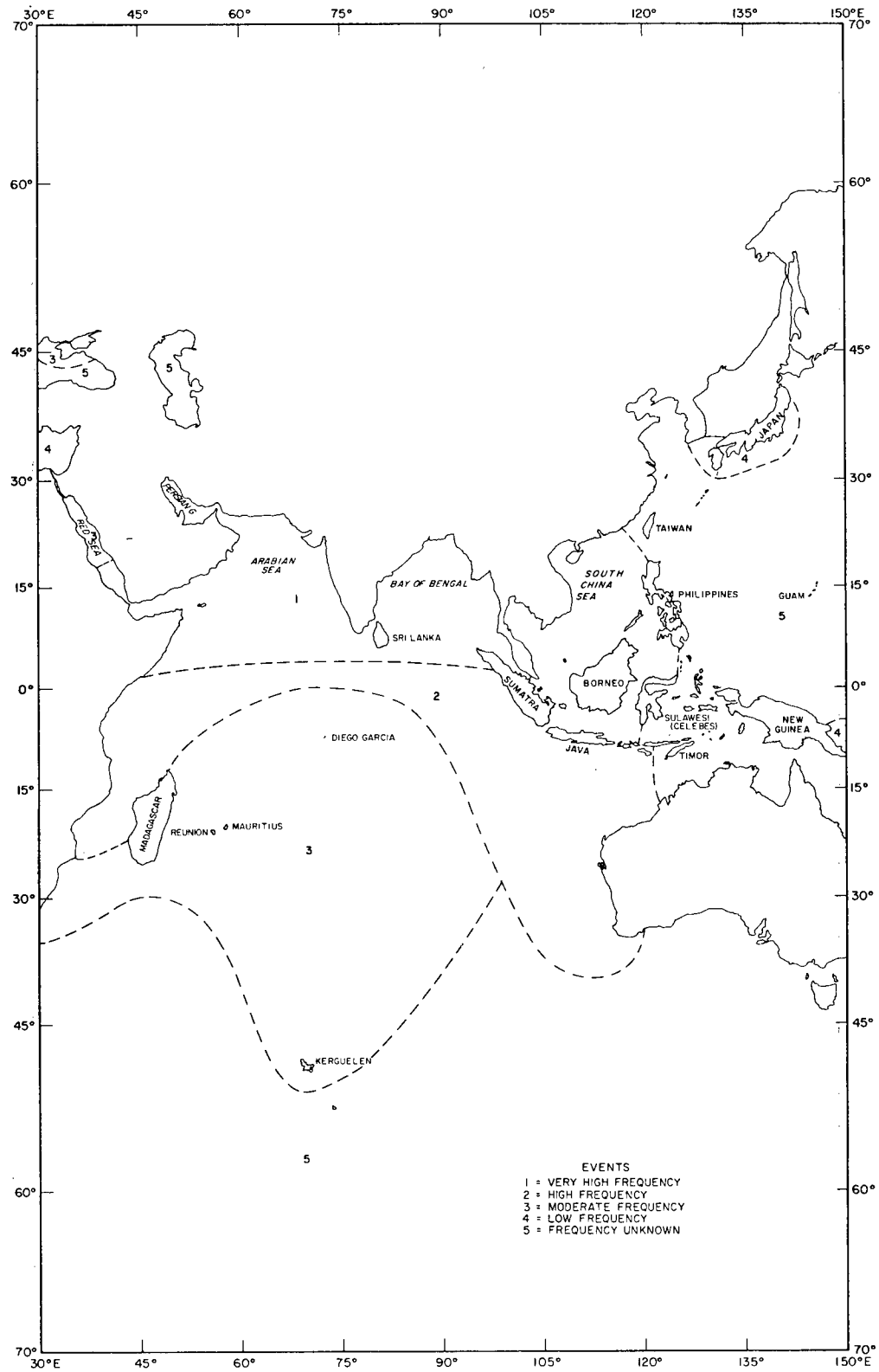


Fig. 26 — Frequency of bioluminescence encounters in the Western Pacific and Indian Oceans, Jan. through Mar.

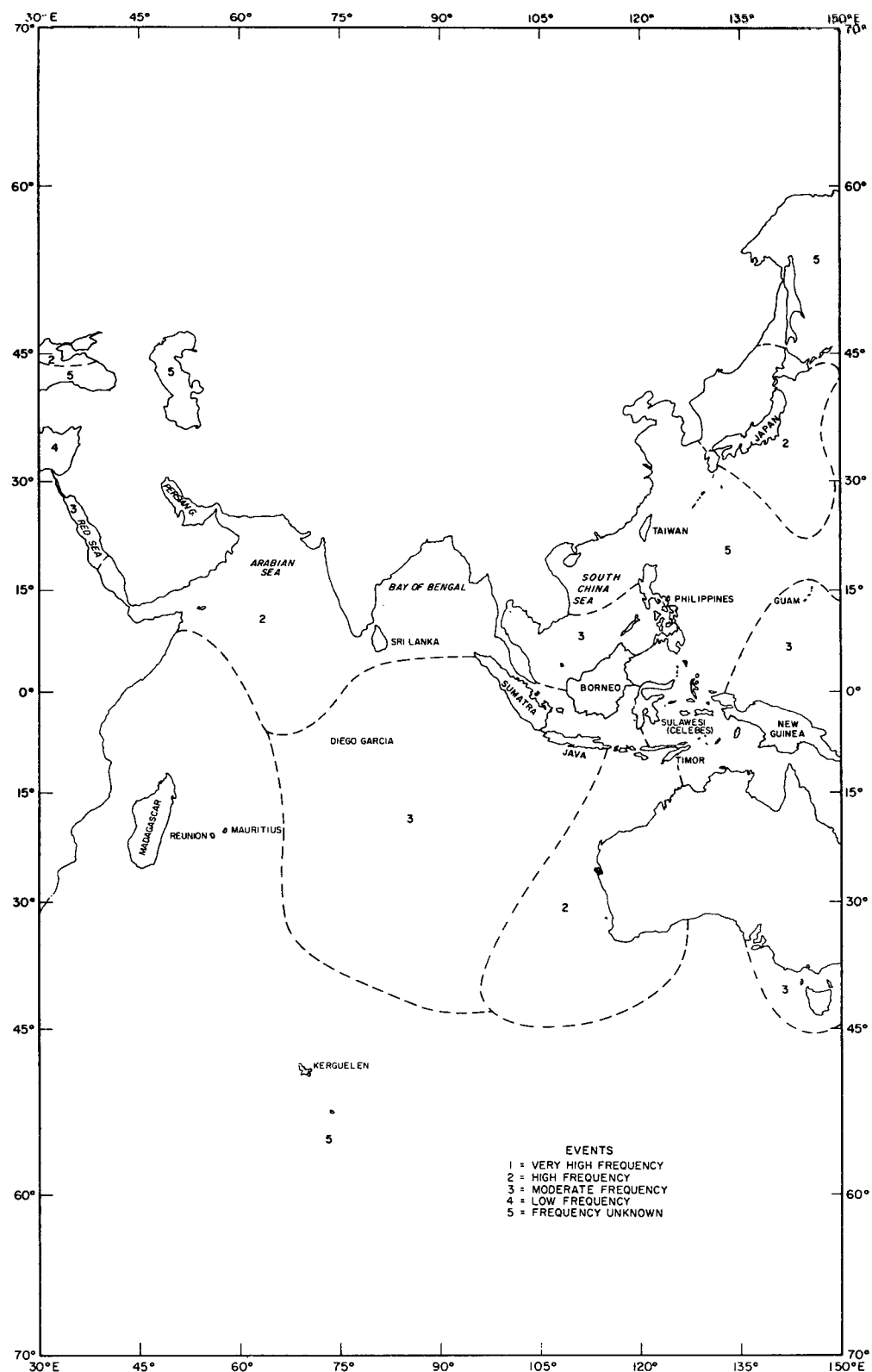


Fig. 27 — Frequency of bioluminescence encounters in the Western Pacific and Indian Ocean, Apr. through June

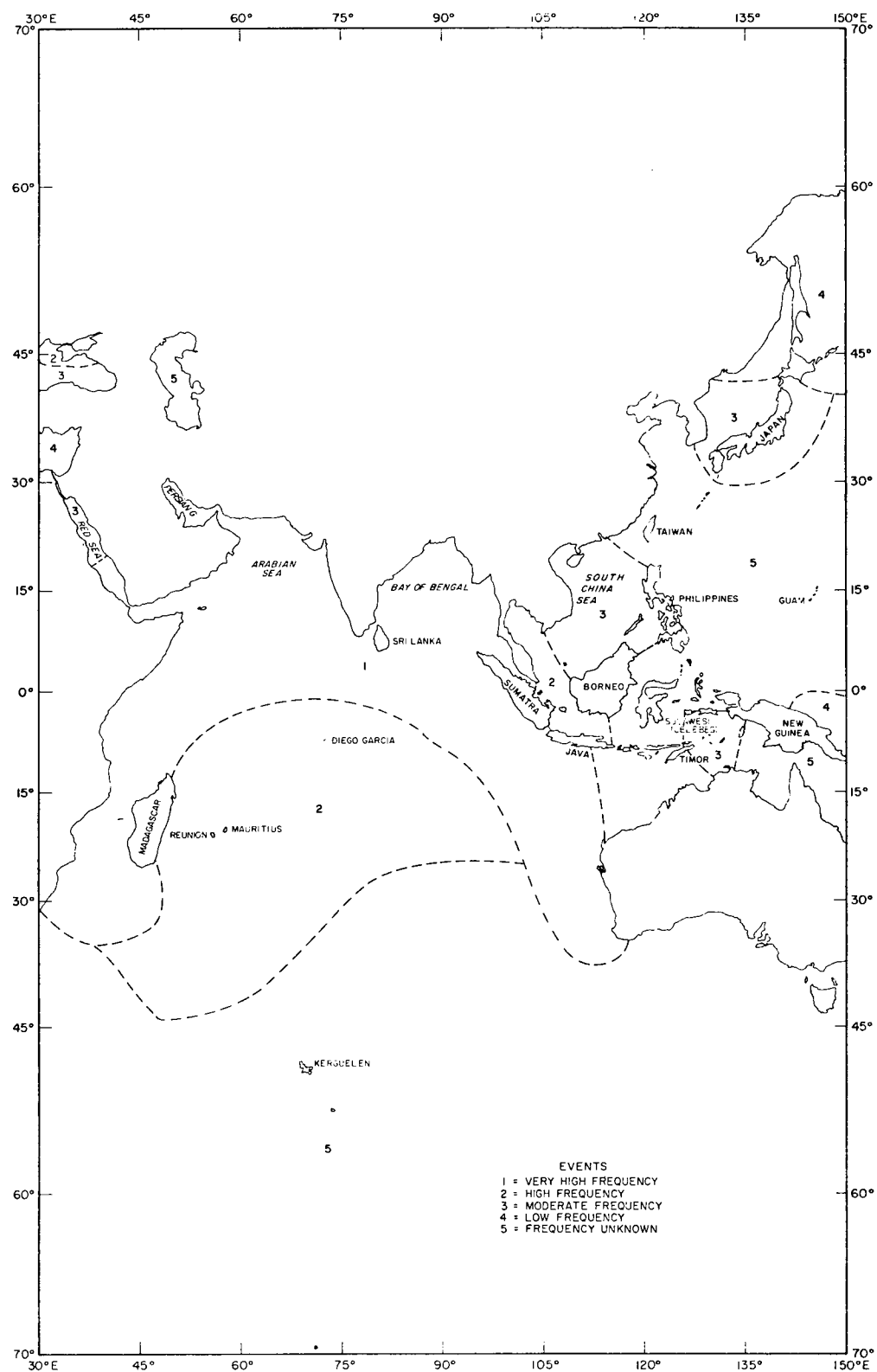


Fig. 28 — Frequency of bioluminescence encounters in the Western Pacific and Indian Ocean, July through Sept.

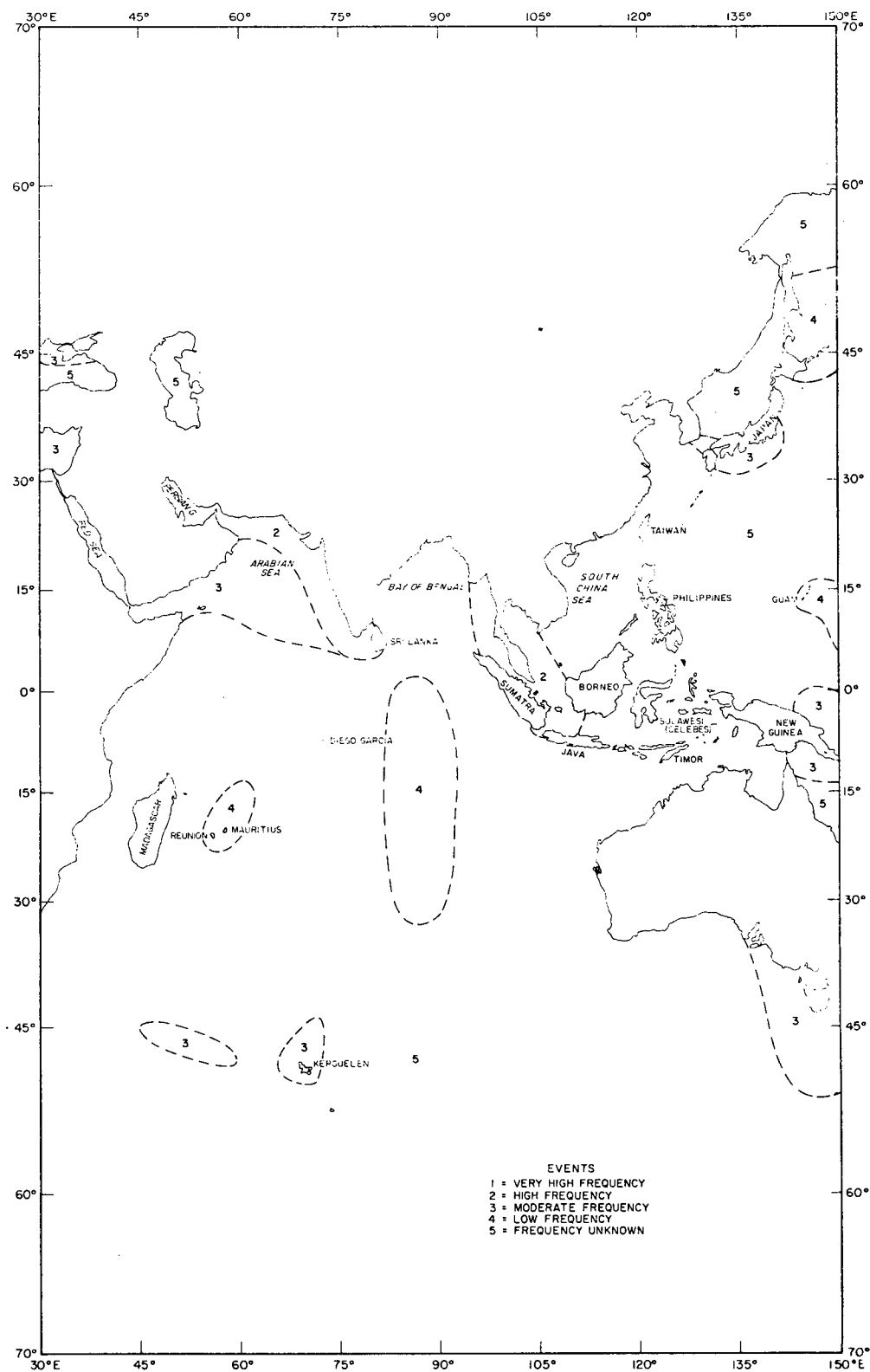


Fig. 29 — Frequency of bioluminescence encounters in the Western Pacific and Indian Oceans, Oct. through Dec.

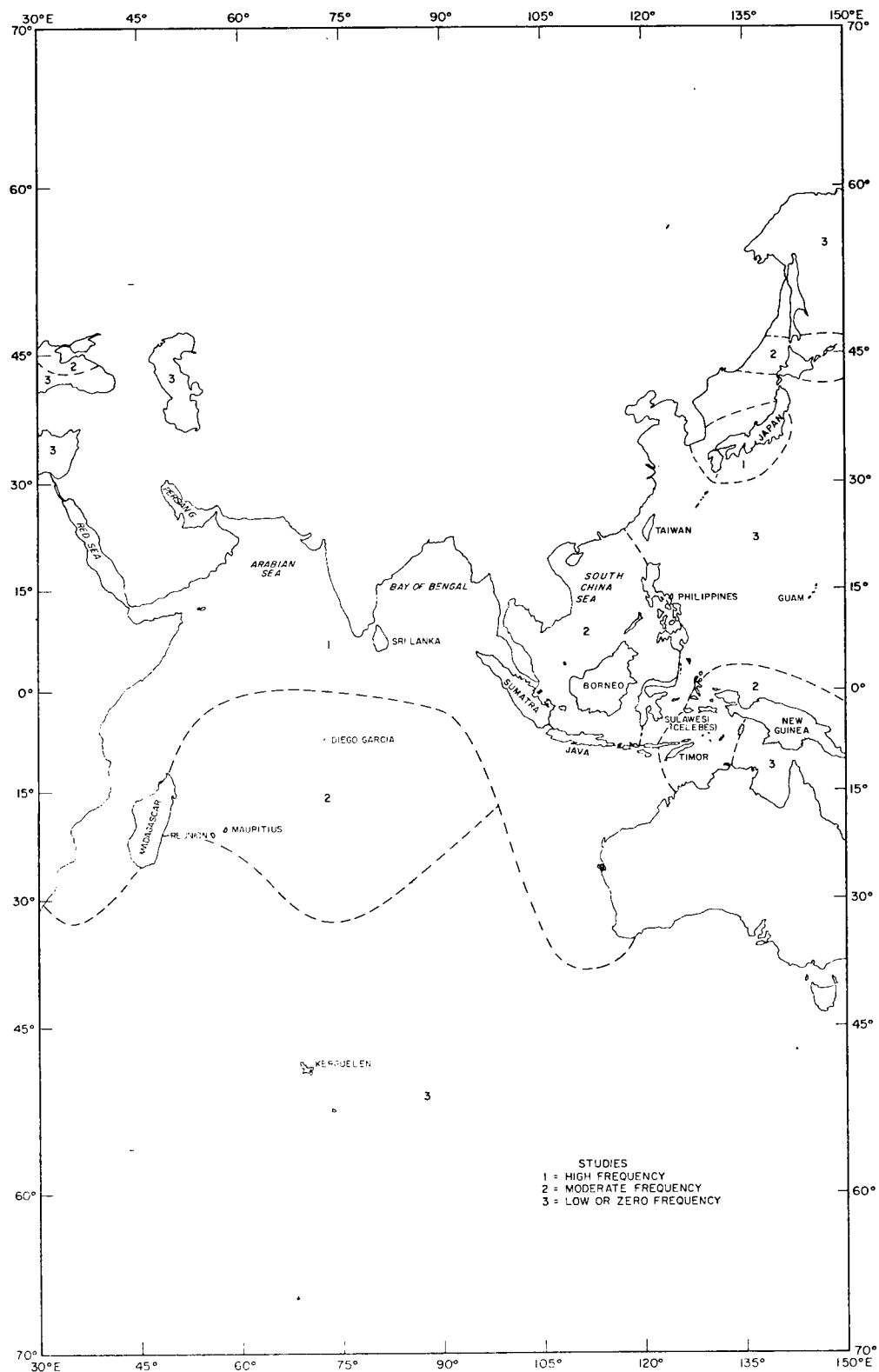


Fig. 30 — Frequency of bioluminescence reports in the Western Pacific and Indian Oceans

strength and upwelling due to the Southwest Monsoon. Staples [17], Tett and Kelly [3], and Lynch [1] suggested a secondary bioluminescence maximum in January through February, corresponding to upwelling induced by the Northeast Monsoon. However, both this upwelling and the consequent bioluminescence are much less than that due to the Southwest Monsoon.

For the remainder of the Indian Ocean few reports are available. Lynch [1] analyzed the taxonomic data of the International Indian Ocean Expedition and found bioluminescent organisms to be very common throughout the studied region and at all times of the year.

A special word is in order about luminous displays in the Arabian Sea and its environs. This area is one of the richest in the world for displays of the "phosphorescent wheel" and "milky sea" types. Only the Strait of Malacca—South China Sea area approaches the Arabian Sea in terms of number of displays. Neither the causative organism(s) nor the triggering mechanism(s) of these displays have been identified. Herring [4] described several types of displays and discussed possible causative organisms. Turner [15,16] and Staples [17] also described various types of displays, and Turner showed that most milky seas in the northern Arabian Sea occur in August, while Staples found that most phosphorescent wheels in the same area appeared from April through June.

Many descriptions of phosphorescent wheels exist, among them Tydeman [22], Termijtelen [23], Rodewald [24], Kalle [20,21], and Hilder [25], who also offer tentative explanations for their occurrence. Tydeman [22] and Termijtelen [23] suggest that the wheels are due to optical illusions created by the motion of the ship and the interaction of the bow wave of the ship with existing waves in a patch of bioluminescence. This theory has been mathematically explored by Verploegh [26], who also considered parallax resulting from the position of the viewer. Kalle [20,21] suggested that wheels and "erupting balls" are triggered by seismic disturbances from underwater earthquakes or volcanos. Hilder [27] observed bioluminescent streaks apparently triggered by ship radar. Because of this observation he suggested [25] that wheels are triggered by electromagnetic anomalies due to sunspots or movement of ships through the earth's magnetic field. Rodewald [24] described an extremely unusual phenomenon, phosphorescent wheels appearing above the sea surface. He suggested that these were caused by luminous microorganisms sucked into the atmosphere with water droplets as aerosols. None of these suggestions has been proved. A discussion of wheels along with suggested research into their causes appears in Lynch [28].

STATISTICAL CONSIDERATIONS

All studies of the patterns of bioluminescence in the oceans have suffered from a bias toward heavily travelled sea lanes. A large number of reports from an area may represent a high level of bioluminescence or it may represent the presence of many ships. Turner [15,16] made the first attempt to correct for this factor by defining a coefficient equal to the percentage of the world total of reports which came from a given area divided by the percentage of the world total of observing ships in that area. He derived his estimate of these percentages by limiting his data to that provided by the Voluntary Observing Fleet from 1920-1938. These ships systematically made four sets of meteorological observations per day and reported the data to the British Meteorological Office along with observations of any unusual phenomena such as bioluminescence. By restricting his data base in this manner, Turner could know the exact numbers and locations of reporting ships. Thus, he could calculate his coefficient and eliminate the effects of ship traffic from his comparisons of the relative frequencies of bioluminescence occurrences in given areas. Because of the limited number of reports, Turner felt that the smallest reliable unit for this kind of analysis was a 10°-Marsden square. Moreover, as Turner pointed out, there are several defects in this method. First, it is based on the assumption that if twice as many ships cross an area, they will send in on the average twice as many reports. Second, there is no way to correct for the passage of a ship through a corner of a square between observations or during the day. However, since this objection applies equally throughout the world, Turner felt that it did not invalidate the method for comparing regions. Third, in places where ship traffic is very heavy, potential

observers may be fully occupied with ship handling and observations may not be made or recorded. Fourth, the correlation between the number of ships and the number of reports becomes unreliable when the shipping density is low, because unavoidable inaccuracies in the shipping estimates become significant at low densities.

Calculation of the coefficient is possible only if the data base is restricted to a fixed number of ships which make systematic observations. Acceptance of any reported observations makes impossible a reliable estimate of the percentage of the world total of observing ships in an area, because no report will be made if a ship observes nothing. Furthermore, observations are generally recorded and reported from general shipping only if they are unusual and if the observer has the interest to report and knows where to report. The author personally knows of many observations which were not reported because the observers did not know where to go or because they had observed dim bioluminescence so often that they considered it routine. Thus, Turner's method is not suitable for analysis of reports from general merchant or military shipping because the irregularity of the reports creates built-in statistical unreliability.

Now that instruments are capable of detecting bioluminescence not visible to the human eye, another source of statistical unreliability has been introduced. Observers using such instruments will obviously see more bioluminescence than those not using them. Thus, it becomes impossible to compare results between the two kinds of observers.

This report suffers from all of the above statistical problems. For that reason no attempt has been made to attach numbers to any of the areas of occurrence outlined on the maps. A high frequency of occurrence simply means that one will likely encounter bioluminescence much more often than moderate frequency would suggest. However, to give some absolute value to the frequency categories used in the maps, the author suggests that the category of "Moderate Frequency" means the constant presence at night of instrumentally measurable bioluminescence, and that "Very High Frequency" might mean optically visible displays occurring once or twice a week. One should also realize that the borders of the luminous regions categorized on the maps are imprecise, and temporal changes occur gradually and not abruptly on the first day of each quarter. The maps showing the frequency of reports have been included to give some indication of the reliability of the frequency of encounter data. Data from areas with high reporting frequencies are more reliable than data from areas with low reporting frequencies. Thus, the encounter estimates from heavily travelled shipping lanes are good, in spite of the statistical problems, while those from little-explored regions may be poor.

CORRELATIONS

Correlations have been postulated between bioluminescence occurrences and regions of high marine productivity [5,18]. This is believed to be largely due to luminous dinoflagellates and occurs most often in shallow waters. The connection between coastal displays off California and luminous dinoflagellates was shown early by Allen [19]. Luminous dinoflagellates also occur frequently, but not always, in red tides. However, the correlation with highly productive regions is not absolute. Kelly and Tett [5] and Lynch [18] have cited exceptions to the theory. The relationship between productivity and bioluminescence may be highly complex [3], but its exact nature is currently unknown.

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REFERENCES

1. R.V. Lynch, "The Occurrence and Distribution of Surface Bioluminescence in the Oceans During 1966 through 1977," NRL Report 8210, 1978.
2. E.N. Harvey, *Bioluminescence*, Academic Press, N.Y., 1952.
3. P.B. Tett and M.G. Kelly, "Marine Bioluminescence," *Oceanog. Mar. Biol. Ann. Rev.* **11**:89-173, 1973.
4. P.J. Herring, "Observations of Bioluminescence at Sea," *Mar. Obs.* **46**:176-183, 1976.
5. M.G. Kelly and P.B. Tett, "Bioluminescence in the Ocean," in *Bioluminescence in Action*, P.J. Herring, ed., Academic Press, N.Y., pp. 399-417, 1978.
6. G.D. Hickman and R.F. Staples, "Bioluminescence of the World's Oceans: Annotated Bibliography," Applied Science Technology Report AST-R-03879, 1979.
7. G.D. Hickman, R.F. Staples, and R.V. Lynch, "Bioluminescence of the World's Oceans: Technical Assessment," Applied Science Technology Report AST-R-080880, 1980.
8. H.T. Smith, "Phosphorescence of the Sea," *Mar. Obs.* **3**:193-196, 1926.
9. H.T. Smith, "Phosphorescence of the Sea," *Mar. Obs.* **8**:230-234, 1931.
10. M.V. Stukalin, "Bioluminescence of the Okhotsk Sea," *Vest. dal'nevost. Fil. Akad. Nauk SSSR* No. 9, pp. 137-139 (USHO Trans. 160), 1934.
11. Anonymous, "Meerleuchten im Arabischen Meer," *Seewart* **8**:12-18, 1939.
12. R.V. Lynch, "Bioluminescence in and near the Arabian Sea," NRL Letter Report 4351-78, 1980.
13. W. Glahn, "Meerleuchten im Atlantischen Ozean," *Seewart* **12**:17-25, 1943.
14. V.V. Murina, "Luminescence in the North Sea," *Priroda*, No. 12, p. 116 (USHO Trans. 22), 1954.
15. R.J. Turner, "Notes on the Nature and Occurrence of Marine Bioluminescence Phenomena," National Institute of Oceanography Internal Report B4, 1965.
16. R.J. Turner, "Marine Bioluminescence," *Mar. Obs.* **36**:20-29, 1966.
17. R.F. Staples, "The Distribution and Characteristics of Surface Bioluminescence in the Oceans," Naval Oceanographic Office Report TR-184, 1966.
18. R.V. Lynch, "The Distribution of Luminous Marine Organisms," *Proc. Naval Oceans Systems Center Workshop on Bioluminescence* (In press).
19. N.I. Tarasov, *Luminescence of the Sea*, Akad. Nauk SSSR, Moscow (Trans. M. Slessers, 1957, US Navy Hydrographic Office) 1956.
20. K. Kalle, "Die rätselhafte und 'unheimliche' Naturerscheinung des 'explodierenden' und des 'rotierenden' Meeresleuchtens—eine Folge lokaler Seebeben?" *Deutsche Hydrog. Zeits.* **13**:49-77, 1960.

21. K. Kalle, "Wheels of Light," *Sea Frontiers* **15**(2):116-122, 1969.
22. G.F. Tydeman, "Phosphorescent Wheels," *Mar. Obs.* **9**:32, 1932.
23. J.W. Termijtelen, "Phosphorescent Wheels," *Mar. Obs.* **20**:229-232, 1950.
24. M. Rodewald, "Phosphorescent Wheels," *Mar. Obs.* **24**:233-234, 1954.
25. B. Hilder, "Marine Phosphorescence and Magnetism," *Navigation (J. Aust. Inst. Navigation)* **1**:43-60, 1962.
26. G. Verploegh, "The Phosphorescent Wheel," *Deutsche Hydrog. Zeits.* **21**:153-162, 1968.
27. B. Hilder, "Radar and Phosphorescence at Sea," *Nature, London* **176**:174-175, 1955.
28. R.V. Lynch, "Problems and Opportunities Connected with Marine Biological Phenomena," in *Advanced Concepts in Ocean Measurements for Marine Biology*, F.P. Diemer, S.J. Vernberg, and D.Z. Mirkes, eds., University of South Carolina Press, Columbia, SC, pp. 245-255, 1980.
29. W.E. Allen, "'Phosphorescence' in the Sea," *Naut. Gaz.*, Aug. 26, pp. 10 and 16, 1939.